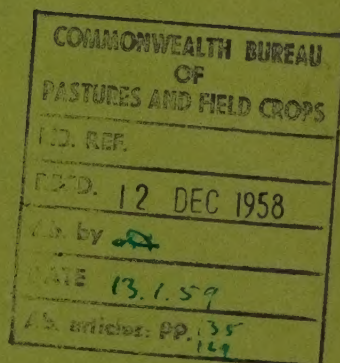


# **BULLETIN OF THE RESEARCH COUNCIL OF ISRAEL**

## **Section D BOTANY.**

*Bull. Res. Council of Israel. D. Bot.*

Continuing the activities of the  
*Palestine Journal of Botany*,  
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# ✓ THE CORRELATION BETWEEN ROOT AND SHOOT GROWTH OF LUCERNE

## I. THE TIME RELATIONSHIP OF ROOT AND SHOOT GROWTH

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### ABSTRACT

The effect of clipping on the growth of the root and shoot systems of lucerne was investigated.

Clipping of lucerne caused a cessation of root growth, while instant shoot growth resulted.

Root growth began after a ten-day interval and at the same time the relative growth rate of the shoot decreased markedly.

The relative growth rate of both shoot and root decreased at the end of the growth cycle of lucerne.

Nodule formation was also delayed by clipping.

### INTRODUCTION

Agricultural practice has established that the stands and crops of lucerne (*Medicago sativa*) are markedly affected by the time of clipping. It has been shown that shoot development depends to a large extent on the root system (Biswell and Weaver 1933, Harrison 1939, Robertson 1933). The root system even determines cold and drought resistance (Grandfield 1935, Robertson 1933). It also seems to affect the ability of lucerne to compete favourably with weeds, or when grown in mixed pasture, with other pasture components (Willard 1951).

It has been shown that the development of the root system is influenced by shoot growth (Grandfield 1935, Nelson 1925, McKee 1916). There is evidence for the dominance of shoot over root development at least in mature plants (Reed and McDougal 1937, Monselise 1947, Marloth 1950).

In spite of these facts very little is known on the exact time relationship between the development of the root and shoot systems and the factors underlying this time relationship.

It is, therefore, necessary to find out whether a competition between shoot and root growth exists and what are the nutritional relationships between root and shoot growth. It is the aim of this and the following paper to clarify some aspects of this problem.

\* Present address: Department of Botany, The Hebrew University of Jerusalem.

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## MATERIAL AND METHODS

The experiments were carried out on three year old plants of *Medicago sativa* var. *peruviana* grown on field plots of a friable loamy clay in the Coastal Plain of Israel. The density of the stand was medium.

In Israel, lucerne is grown under irrigation for hay during the major part of the year. The most vigorous growth occurs during spring and autumn, when the plants may be clipped every 25-30 days.

In our experiments the clipping was done on the 4th of June, 1954, and shoot and root growth measured on eight days in June: on the 9, 11, 14, 16, 18, 20, 23, 27, 30 of June.

*Measurements of roots*

The simplest method of measuring root growth is to dig up representative soil samples and count and measure the newly developed roots (Reed and McDougal 1937, Monselise 1947). This method is unsuitable for lucerne, as its new roots become suberized very rapidly and undistinguishable from the old ones.

The following method was found to be satisfactory. Immediately after clipping, a hole was dug close to the tap root, and a flower pot filled with moist soil was inserted into the hole in a horizontal position, with its open side towards the tap root (Figure 1). The pot was firmly pushed into the surrounding soil and the hole refilled.

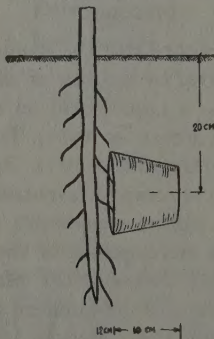


Figure 1

Method of following lateral root initiation and growth.

Whenever root growth determinations were made, a sample pot was dug out and the roots inside counted and measured. It is obvious that all roots within the pots developed after the clipping.

When using this method, many roots were cut off by digging. It was suspected that this might influence root growth and development. A large number of comparisons between the method adopted and that of Reed and McDougal (1937) and Monselise (1947) were made to determine whether the appearance of new roots was affected by the treatment. In no case, however, could a significant difference be found.



As the coefficient of variability of root growth was estimated to be about 40%, at least 25 replicates of every measurement were necessary in order to show the significance of a 15% difference (Snedecor 1946). As measurements were made on eight different days, 25 randomized blocks containing nine plots each were designed. The plot size (50×100 cm) enabled treatment without interference with the plants in the neighbouring plot. From every plot one experimental plant was selected at random.

### *Measurements of shoots*

The method of Heath (1937) for shoot measurements was used. Elongation gives an adequate picture of shoot growth in general. The elongation of eight shoots from each of the 25 selected plants was followed during the experiment. The mean values given are, therefore, based on 200 measurements.

Similar experiments on a smaller scale had been carried out during the previous year, with essentially the same results.

### RESULTS AND DISCUSSION

The total growth of shoots and roots expressed as the logarithm of length is shown in Figure 2. It will be seen that whereas shoot growth begins immediately, roots do not show any elongation until the eighth to eleventh day after clipping.

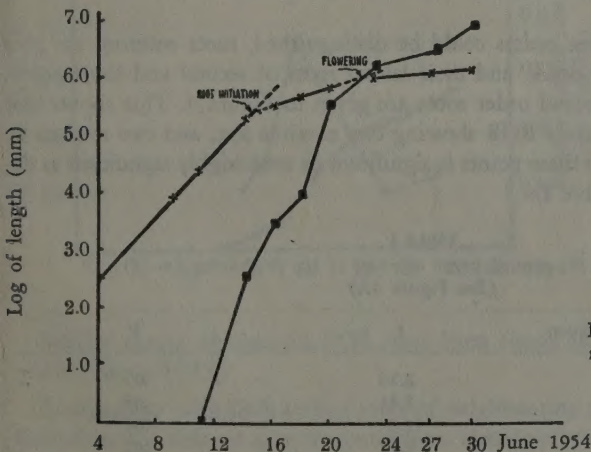


Figure 2  
Logarithmic curve of lucerne root and shoot growth.  
× Shoots  
■ Roots

Furthermore, the shoot growth curve is composed of three straight lines which indicate that there are three periods of constant relative growth rate — RGR (Brody 1945). The relation between RGR and time is given in Figure 3 which is based on the same measurements as Figure 2. It will be seen that there exist three RGR at different levels, every level being approximately one third the height

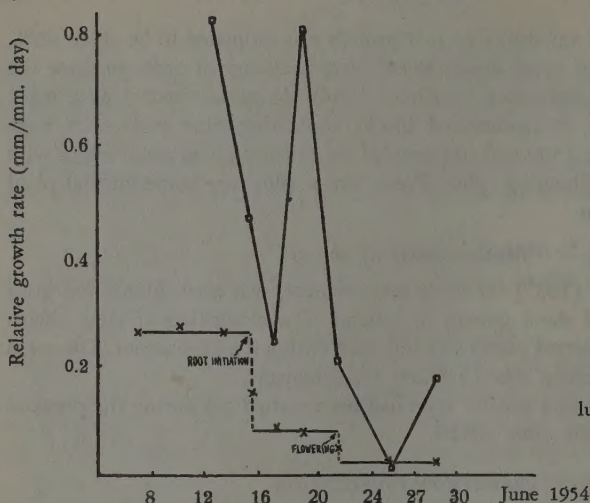


Figure 3  
Relative growth rate of  
lucerne roots and shoots.

× Shoots

□ Roots

of the preceding one. The transitions between the RGR levels are steep and are presumably connected with some physiological phenomena. During the first transition, initiation of root growth takes place, while, during the second, flowering occurs.

Secondary roots of three orders could be distinguished, roots entering the pots being considered of first order, and their lateral roots of second and third order. The RGR of first and second order roots are given in Figure 4. This shows that roots of the first order have a RGR showing two maxima a, c, and two minima b, d. The difference between these points is significant or even highly significant as determined by the test (Table I).

TABLE I

*Statistical analysis of the growth curve of roots of the first order ( $n-2=48$ )*  
(See Figure 4A)

Differences between	t		P
a — b	2.56	>	.05
b — c	2.41	>	.05
c — d	11.3	>	.01
d — e	1.18	<	.05

The growth curve of roots of the second order did not show the same picture. But as only short roots appeared, due to the nature of our experimental design, this curve cannot be compared with that of first order roots. When, however, first and second order roots are measured together, there emerges a curve very similar to that of first order roots.



The growth curve can also be presented differently, as two straight lines, indicating that the first period has a high and steady RGR and the second period a low one (Figure 4).

Hammond and Kirkham (1949) found similar growth curves with three periods in soya and with four periods in maize. Flowering occurred in two of the transition periods. The above authors found it desirable to divide the whole growth curve into separate sections, each of which could be expressed by an exponential function. We have found that a similar treatment is applicable to our results.

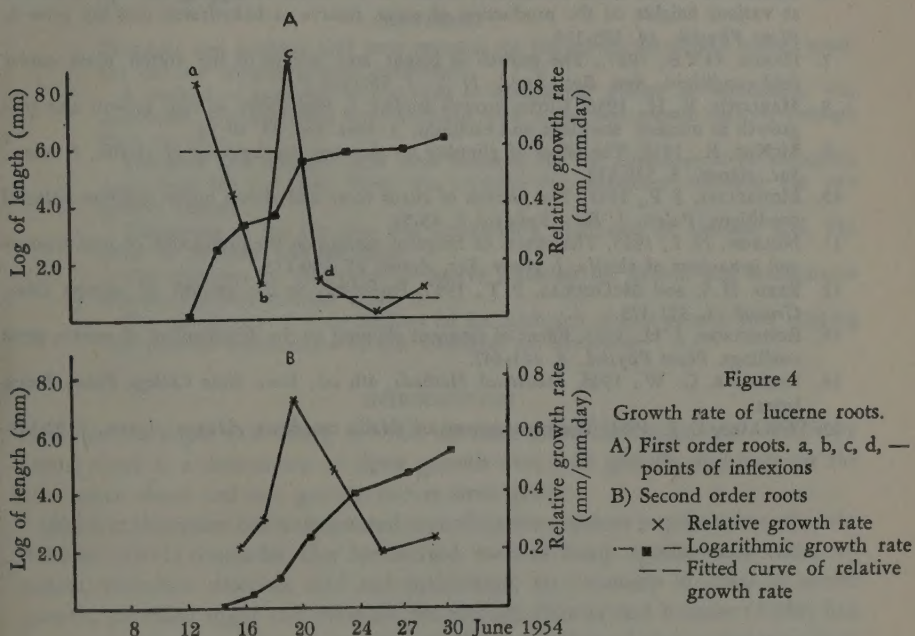


Figure 4

Growth rate of lucerne roots.

A) First order roots. a, b, c, d, — points of inflexions

B) Second order roots

× Relative growth rate  
—■— Logarithmic growth rate  
--- Fitted curve of relative growth rate

Similar abrupt changes in RGR have been found in animals and micro-organisms (Brody 1945).

Comparison with undisturbed roots of neighbouring plants showed that nodule formation was delayed even in young roots already present at the time of clipping. It appears, therefore, that nodule formation is not determined by the presence of young roots only, but also by shoot development. Bonner (1950) has pointed out that nodule formation depends on growth factors coming from the shoots. This aspect of the work will be discussed elsewhere.

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# THE CORRELATION BETWEEN ROOT AND SHOOT GROWTH OF LUCERNE

## II. NUTRIENT RELATIONS OF ROOTS AND SHOOTS

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### ABSTRACT

Thiamine and nicotinic acid were essential for the growth of excised lucerne roots, but did not support growth indefinitely.

A method of growing the tap roots of decapitated plants in vermiculite was developed. The tap roots were supplied with sugar and growth factors, through their cut ends.

Thiamine and nicotinic acid were essential for the development of secondary roots from the tap roots. There was evidence for antagonism between the two growth factors.

Thickening of the tap root was significantly stimulated by nicotinic acid. The effect of thiamine was less clear.

The efficiency of utilization of reserve materials for growth and maintenance was increased by nicotinic acid.

The significance of these findings on the inhibition of root growth after clipping and possible explanations of this inhibition are discussed.

### INTRODUCTION

In a previous paper (Ginzburg 1958) it has been stated that in lucerne (*Medicago sativa*) there is a dominance of shoot growth over root growth, and data on the time when shoot and root growth occurs were given.

Much information has accumulated regarding the nutrient requirements of roots. Robbins (1951) concludes that for excised roots of many species only three vitamins, thiamine, nicotinic acid and pyridoxine, are necessary in order to secure growth, provided sugar and minerals are present. Bonner and Bonner (1948) had previously arrived at the same conclusion. They also showed that in tomatoes thiamine is synthesized mostly in mature leaves and transferred to the region of active growth. The same appears to be the case for nicotinic acid. Bonner (1942) showed that when tomato plant is girdled, thiamine accumulates in the phloem, above the place of interruption, together with organic foodstuffs. Crafts (1951) also assumes transport of thiamine in the phloem together with other metabolites. Bonner (1942) showed an increase in thiamine in the roots of debudded plants. This may indicate competition between root and shoot growing points and the young leaves for thiamine.

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White (1938) and Bonner (1940) showed that isolated roots of lucerne can grow on synthetic media containing minerals, sucrose, thiamine and nicotinic acid. The present author investigated the influence of thiamine and nicotinic acid on whole tap roots. At the same time the experiments of Bonner (1940) and White (1938) on the influence of thiamine and nicotinic acid on excised root tips were repeated.

## METHODS

### 1. Root culture

The nutrient solutions were prepared from a mineral stock solution according to White (1943) to which were added nicotinic acid and thiamine. The solutions were sterilized for 15 minutes at 15 lbs pressure. The roots were grown in 100 ml Erlenmeyer flasks containing 40 ml nutrient solution.

The seeds used (*Medicago sativa* var. *peruviana*) were sterilized in 0.5%  $\text{HgCl}_2$  for twenty minutes, rinsed with sterile water and germinated in Petri-dishes on filter paper for 48 hours at  $25^\circ\text{C}$ . At the end of this period the roots were cut 10 mm from the tip. Only uniform root tips were used for the experiment. The tips were transferred to the following solutions:

1. White's basic solution + thiamine 0.1 p.p.m. (Treatment T).
2. White's basic solution + nicotinic acid 0.5 p.p.m. (Treatment N).
3. White's basic solution + nicotinic acid + thiamine (Treatment TN).
4. White's basic solution alone (control).

Twelve replicates, i.e. twelve flasks were used for each treatment. The roots were kept at  $25^\circ \pm 1^\circ\text{C}$ .

At weekly intervals the length of the roots was measured and the apical 10 mm cut off and transferred to a fresh solution.

### 2. Growth of the intact root system and application of vitamins and sugars

Intact plants were dug up from the field, the adhering soil was removed by washing, and the tops were cut off immediately below the crown. To the upper part of the remaining tap root glass tubes about 8 cm long were tightly fitted by means of a piece of elastic rubber tube (Figure 1). The roots were then planted in boxes  $80 \times 80 \times 50$  cm, filled with vermiculite to which were added mineral solutions as specified later. The use of vermiculite ensured constant temperature (fluctuation  $\pm 1^\circ\text{C}$ ).



Figure 1  
Method of supplying nutrients to tap root (modified after Snow 1953).

Conditions of aeration are very favourable in vermiculite. From the real and apparent specific weight we calculated its air capacity. With 108% per weight moisture the total pore space was 73%. The non-capillary porosity, i.e. the air capacity was 54% per volume.

Moisture constants were measured by the tension plate method and found to be :

Pw  $\frac{1}{3}$  atm 160%

Pw 15 atm 78%

By means of extrapolation, the moisture content at field capacity and wilting point were calculated (Rubin 1953) :

Pw (F.C.) 100%

Pw (W.P.) 64.8%

35.2% available water range.

The amount of available water, therefore, is very large.

Hewitt's (1952) mineral nutrient solution was used throughout the experiment at a pH of 5.6.

After a single thorough wetting of the vermiculite with the mineral solution, no further application was found to be necessary.

The concentration and the composition of sugar and vitamin solution were chosen so as to approximate the natural composition of the plant sap as closely as possible.

Rosenberg (1947) has shown that leaves of various families contain a constant amount of thiamine. This he found to be about 25 I.U./100g fresh weight=75% thiamine·HCl. In our case, the fresh weight of leaves of a single plant is about 20-100g. To every root 5ml of p.p.m. thiamine solution were applied in order to arrive at the amount of 25% per plant. The concentration of nicotinic acid was 10 p.p.m. The vitamins were applied in a solution of phosphate buffer with pH 5.5. The concentration of sucrose was 10%. The solution in the glass tubes was changed daily.

The following treatments were used :

Treatment	Solution
T	Thiamine 5 p.p.m.
ST	Thiamine 5 p.p.m. + Sucrose 10%
N	Nicotinic acid 10 p.p.m.
SN	Nicotinic acid 10 p.p.m. + Sucrose 10%
TN	Nicotinic acid 10 p.p.m. + Thiamine 5 p.p.m.
STN	Nicotinic acid 10 p.p.m. + Thiamine 5 p.p.m. + Sucrose 10%
S	Sucrose 10%
C	Control

Every treatment was applied in 8 replicates. The design is analogous to that of a three factorial field experiment. Accordingly, every box containing vermiculite and mineral solution was divided into eight blocks with eight "plots" each, and the treatments were assigned to the plots within the various blocks at random.

The experiments were carried out in two series: One series with two year old plants and the second with three year old ones. As in the first series only variation in dry weight of secondary roots was determined and, as a number of replicates had to be discarded during the experiment, less significance will be attributed to the results of this series.

Growth was measured in tap roots by increment of: (a) diameter; (b) volume; (c) dry weight.

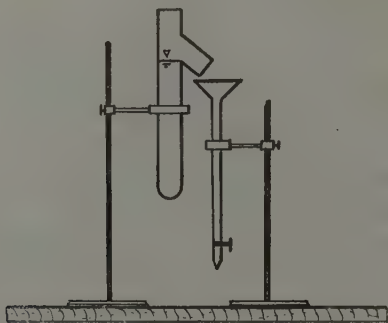


Figure 2  
Method for measuring volume of roots.

As the initiation of secondary roots took place only after the beginning of the experiments, it is obvious that their final dry weight may be used as a criterion of their growth. In the tap root, however, the dry weight at the beginning of the experiment has been determined indirectly by examination of the correlation between root dry weight and root volume. This was found to be a very strict one allowing the calculation of initial dry weight. Volume measurements were made by help of a glass tube with an open side-arm and a burette (Figure 2). The root diameter was measured by a micrometer. The statistical analysis of results has been carried out according to the factorial design of the experiments by analysis of variance (Snedecor 1946, Cochran and Cox 1950).

## RESULTS

### 1. Root culture

As is evident from Tables I and II, addition of T and N together gives in every transfer a significantly higher growth increment than the control.



TABLE I  
Weekly growth increment (in mm) of root

	Thiamine	Nicotinic acid	Thiamine + Nicotinic acid	Control	F observed	F calculated	Coefficient of variability
First transfer	38.9	29.6	34.0	19.3	2.67*	2.57	66%
Second transfer	13.3	18.3	34.1	2.1	5.60**	2.79	155%
Third transfer	2.2	2.7	11.2	1.0	3.36*	2.89	145%
Fourth transfer	1.8	0.4	3.6	2.0			

\*  $P < 0.05$ \*\*  $P < 0.01$ 

TABLE II  
Statistical analysis of root culture

	Significant difference 0.05%	Difference
<i>First transfer</i>		
Control vs. TN	14.3	14.7*
" " T	14.9	19.6**
" " N	14.8	10.3
<i>Second transfer</i>		
Control vs. TN	19.6	32.0*
" " T	15.0	11.2
" " N	17.3	16.2
<i>Third transfer</i>		
Control vs. TN	7.2	10.2*
" " T	6.4	1.2
" " N	6.0	1.7

\*  $< 0.05$ \*\*  $< 0.01$ 

Addition of T or N alone gave in both cases an increase in growth, the significance of which is doubtful. In either treatment growth was more marked than in the controls. However, the growth increment already decreased after the second transfer, as does that of the controls. Only when nicotinic acid and thiamine were added together, did the growth increment remain steady throughout the first two transfers.

It may be concluded, therefore, that addition of both T and N is required for maintaining growth in lucerne roots.

It must be mentioned that we did not succeed in maintaining a steady growth rate for more than two transfers, in contrast to Bonner (1940) and White (1938). The differences in results may be due to a number of factors.

1. There was a slight difference in the composition of the mineral solution.
2. There may have been an effect of pH on the solution.
3. Lastly the variety of lucerne differed from that used by Bonner and White.

The growth rate obtained was 5.8 mm per day as compared with 13 mm per day obtained by Bonner and 6.3 mm per day by White.

## 2. Tap-root system

### 1. Growth of secondary roots

Two series of experiments on the growth of secondary roots were arranged (Table III). Growth of secondary roots is here expressed as an increase in dry weight in mg. There was no correlation between the dry weight of the secondary roots and the initial dry weight of the tap roots.

TABLE III  
Data on tap-root system

	T	ST	N	SN	TN	STN	S	Control	Significant difference
<i>Series 1</i>									
Root dry weight increment (in mg)	63.4	13.4	22.7	12.6	18.0	13.5	14.0	7.7	31.6
<i>Series 2</i>									
Root dry weight increment (in mg)	6.0	45.6	28.5	42.8	14.4	17.2	13.2	4.8	22.5
Increment of diameter of tap roots (in %)	13.1	16.9	11.6	20.3	15.3	23.4	13.7	10.2	7.08
Loss of dry weight of tap roots (in %)	16.8	19.9	21.6	9.0	14.9	19.6	8.6	29.5	10.2

In both cases the water control — roots grown without addition of vitamins and sugar — showed only a very slight growth. In comparison with them the most favourable treatment gave almost tenfold increases over the controls.

A comparison between the two series shows:

1. In the first series, only T rendered highly significant results, whereas the influence of N was apparent, but not statistically significant. In the second series both treatment with T and N had significant effects when in combination with S.

2. In the first series, addition of sugar to T had no favourable effect, whereas in the second one, addition of sugar always increased growth. This may be explained by a different carbohydrate level in the roots used in the two experiments,

as they were taken at different times after harvesting (Grandfield 1935). In the first case, the roots were examined a few days after harvest, when the carbohydrate level was still high, whereas in the second case they were collected and tested a short time before flowering when the carbohydrate level in the root was at a minimum.

3. In series 1, a negative effect of sugar was found in all cases. This effect was, however, significant only in the case of T. No explanation for this effect could be found.

4. In all cases, the combination of T and N, with or without the addition of sugar, results in less growth than a treatment of T or N alone. In other words, there is antagonism between thiamine and nicotinic acid at the concentrations used.

## 2. *Thickening (Secondary growth)*

In our second series of experiments the increase in thickness of the tap roots was also determined. The initial and final diameters of the tap root were measured 2 cm below the point of insertion in the glass tube. As can be learnt from Table III, addition of nicotinic acid causes a highly significant increase in the root diameter. There is only a small effect of thiamine.

## 3. *Loss of dry weight*

Dry weight at the time of its determination is given as percentage of the initial dry weight. In all cases a decrease of dry weight was found (Table III). In the controls this amounted to about 30%, a loss which is about 3.5 times larger than in treatment S or SN (8-9%). An intermediate loss (15-20% was found in the other treatments.

Presumably the loss of dry weight is caused by respiration which supplied the energy for "maintenance" and growth. Growth and loss of dry weight were, however, not correlated. The highest losses occurred in the controls, where growth was very small. SN gave strong growth and very small dry weight losses. T resulted in relatively little growth and moderate dry weight losses. Treatment with sugar produced intermediate growth and very small dry weight losses.

## DISCUSSION

There can be two explanations of the effect of added thiamine and nicotinic acid on roots. As Snell (1951) pointed out, these growth factors as well as others are found in every cell of living organisms. They function as essential components of important enzymatic systems. Their non-occurrence indicates an inability to synthesize them. Snell (1953) and Reed (1953) reviewed the metabolic functions of thiamine and nicotinic acid. Nicotinic acid is a component of some coenzymes which act as acceptors in dehydrogenization of many compounds. Thiamine is incorporated in the co-carboxylase structure. In the process of oxidative decarboxylation of keto-acids, the complex of thiamine-lipoic acid takes part. In one step of



this reaction the DPN, which contains nicotinic acid, also participates. In this case thiamine and nicotinic acid are both required for proper enzymatic activity.

Zemaglis (1952) and Rahn (1952) in their theory of vitamin action explain differently the effect of vitamins added to bacterial cultures. They assume that the main effect of added vitamins is to increase the tolerance of bacteria to their metabolic products. In this way the efficiency of energy to duplicate the cell is greatly increased. This is similar to our findings on the effect of nicotinic acid, and to a lesser extent of thiamine, with regard to their sparing action in loss of dry weight from storage materials in growing roots.

Clipping may cause the deficiency of certain growth factors at the root growth sites. We have shown that thiamine and nicotinic acid are required for root growth. This is immediately evident for secondary root growth. For excised primary roots the requirement becomes evident somewhat later. This points to a physiological difference between the root tips of primary roots of seedlings and those of secondary roots of mature plants which might be different in their content of growth factors. This difference in supply of growth factors might stand in connection with the reversal of root-shoot dominance which occurs during the development of seedlings. Similar results have been obtained by Robbins (1951) for carrot seedlings.

On the other hand, the clipping of the shoots and the subsequent renewed shoot growth may cause the formation or activation of growth inhibitors in the roots. The fact that vitamins and sugars caused resumption of root growth makes this unlikely. If inhibitors should occur, they would presumably originate in the newly sprouting shoots and may consequently be IAA.

Auxin concentration which stimulates shoot growth, inhibits root growth. Thimann (1952), Audus (1953), Weaver and de Rose (1946) have shown that auxin and 2,4-D move from the shoot to the root. The flow of these substances is associated with the nutrient flow in the phloem.

If auxin is indeed the inhibitor of root growth in lucerne, we may ask why its effect disappears after a time, when the relative growth rate of the shoot decreases. At this time there are many growing points in the shoot, and active transport of plastic materials from shoot to root, presumably including auxin, takes place. It is of course possible that the IAA oxidative system in the root or the shoot increases its activity when root growth is renewed, and thus auxin concentration diminishes. A sudden increase in IAA oxidase activity would thus simultaneously stimulate root and depress shoot growth.

The last possibility to be considered is that the shoot dominates over the root due to an advantage in its competition for food materials stored in the root which are moved to the shoot. Loeb (1924) concluded that when growth of a plant organ increases, a flow of food materials to these rapidly growing regions sets in. This will result in a suppression of growth of other competing organs.

Similar conditions prevail in our lucerne experiments. Here, we find a sudden acceleration of shoot growth. The question then arises what is the immediate cause of this sudden acceleration of shoot growth which suppresses root growth. If the root buds can synthesize all its growth factors, growth can begin. It will then draw upon the reserve materials of the roots. If, on the other hand, the root requires growth factors from the shoot and these are not being supplied, then its growth will be suppressed.

Bonner and Bonner (1948) have shown that thiamine is transported only from mature, but not from immature tomato leaves. Comparing the data of Grandfield (1935) and Leukal (1927) on the depletion of reserve material in lucerne tap roots to shoot growth curves, we find that depletion continues, until the RGR of the shoot decreases abruptly. If there is a one-way traffic of reserve materials from the root to the shoot, the shoot growth will depend in its initial stages on the amount of root reserve materials. Grandfield (1935) has pointed out that the lucerne crop is proportional to the amount of root reserves.

The decrease in the RGR and the onset of rootlet growth remain to be explained. When flowering begins, the RGR of both root and shoot decreases abruptly. Here again, the cause may be the diversion of all materials to the reproductive organs. Leukal (1927) has in fact shown a diminished flow of nutrients to the root between the flower bud stage and full bloom.

The physiological differences between primary root tips and secondary ones may be due to differences in the contents of growth factors (thiamine, nicotinic acid or others). We might try to explain the lack of shoot over root dominance in the seedling stage as follows: The presence of growth factors in seedling root tips accelerates their initial growth. As a result, they attract food materials, which causes further acceleration. This might explain the fact that in the seedlings root growth is more intensive than shoot growth.

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# STUDIES ON CROWN RUST AND STEM RUST ON OATS IN ISRAEL

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## ABSTRACT

Recurring crown rust and stem rust epiphytotics cause severe damage to oats in Israel. The first disease usually appears in March, the latter in April. Up to 150 varieties including many introduced from all parts of the globe were tested in the central coastal plain (Mikveh Israel), and in uniform observation nurseries distributed in widely different regions of the country. Varietal trials conducted over a period of 6 years, 1951—1956, proved that the Brazilian variety Saia and the Minnesota selections Minn. II-47-12, and Minn. II-47-17 have been so far very resistant to both oat rusts. Saia is also very suitable for fodder and hay production.

The local oat selection Rehovot showed extremely high resistance to crown rust under field conditions. The so-called Canadian factors for oat stem rust resistance were effective in all tests performed in greenhouses and in field plots at temperatures below 28°C. In the case of *Puccinia coronata avenae*, races 264, 270, and 276 prevailed. Races 264 and 270 were discovered first in Israel. The extremely virulent oat stem rust race 6 comprised about 97 per cent of the identified isolates. The similarity of crown rust races predominant in Israel to those reported from Argentina was emphasized. The importance of the ubiquitous wild oats *Avena sterilis* L. in dissemination of both oat rusts was stressed.

The significance of *Rhamnus alaternus* and *Rhamnus palaestina* as alternate hosts in crown rust life-cycle was discussed.

It is postulated that the prevalence of extremely virulent races of crown rust and oat stem rust in Israel is an outcome of a long lasting process of evolution and struggle for survival.

Cultivation of oats in Israel is severely handicapped by recurring epiphytotics of rusts, particularly by crown rust (*Puccinia coronata* Cda. var. *avenae* Fraser and Led.) and to a lesser degree by stem rust (*P. graminis* Pers. f. sp. *avenae* Eriks. & E. Henn.).

As the importance of oat rust diseases began to be fully appreciated, a better knowledge of the physiologic specialization of the parasitic organisms and of the sources of host resistance became imperative. This investigation was, therefore, undertaken with the purpose of exploring the possibility of introducing resistant varieties and of determining the physiologic races of both crown rust and stem rust, their prevalence and distribution.

## CULTIVATION OF OATS IN ISRAEL

The main purpose of oat production in this country is the supply of green fodder, hay and grain. Our four most common varieties are: Fulghum and Mulga, both

introduced from Australia, Kanota — a Fulghum selection brought from the U.S., and Metualith, of a local or Syrian origin.

Ordinarily, oats are sown in November—December and harvested by the end of May or early June. Small oat fields, cultivated under irrigation, are sown in October. The wild oat species, *Avena sterilis* L., is widespread in all parts of Israel. Its growing season begins in November and ends in May.

#### OCCURRENCE OF RUSTS ON CULTIVATED AND WILD OATS

Crown rust epiphytotics usually set in on cultivated varieties by mid-February or during the first part of March, whereas on wild oats they appear with the first rains, in November, or at the beginning of December. Stem rust incidence on cultivated oats starts by mid-April. In the summer months, when wild oats dry up, stem rust disappears and only in few cases have uredial pustules been detected on wild oat escapes that retained their viability in moist, shady places.

In irrigated fields, particularly in the southern regions of the country — both crown and stem rust may be encountered in November—December.

#### VARIETAL TESTS IN OAT NURSERIES

In the fall of 1951, oat nurseries were planted on the experimental lands of the Mikveh Israel Agricultural School, located about 2 miles south of Tel-Aviv, and also on lands of the Faculty of Agriculture of the Hebrew University, at Rehovot. Varieties from the United States, Argentina, Algeria, Australia, Canada, Denmark, Finland, Morocco, Poland, South Africa, Sweden, Uruguay, and Israel were sown in single 18-foot rows at both nurseries (Table I). Natural rust infections occurred and from early March to mid-May the prevalence, severity, and infection types of both rusts were recorded at least once and sometimes twice each week.

#### CROWN RUST REACTIONS IN 1951-52

Data recorded at the Mikveh Israel nursery in 1951-52 prove that an epiphytotic of crown rust occurred in March, April, and early May, but declined strikingly by mid-May. The disease developed slowly on some varieties and rapidly on others. In March, the rust prevalence varied from 20 per cent on some entries, like Bonda, Camellia, and Mindo, to 100 per cent on the majority of the remaining varieties. In April, however, the crown rust prevalence reached 100 per cent on all varieties and the rust severity generally had increased to maximum for the season. Of the varieties commonly grown in Israel, Fulghum and Metulaith were featured by a high susceptibility, manifested by 65 per cent severity and infection type 4. Kanota displayed the same infection type but of a somewhat lesser severity, estimated as 40 per cent, whereas Mulga showed a maximum severity of 25 per cent. The reaction class for all the aforementioned varieties was considered as susceptible.

The variety Bond and its derivatives, Andrew, Bonda, Camellia, Clinton, and Mindo, were susceptible to crown rust at Mikveh Israel where rust severity reached

0 per cent on Andrew, Bond, Clinton, and Mindo with uredia of the virulent infection type. On Bonda and Camellia the disease severity rated 25 per cent and the pustules were designated as types 3 and 3+ respectively.

Victoria derivatives differed in their reactions to crown rust at Mikveh Israel. Three of them: Letoria, Neosho, and Osage, suffered from crown rust to the extent of 25 per cent severity and type 3 infection. On other Victoria hybrids, such as Boone, Cedar, De Sota, Fultex, Ranger, Tama, Texas, Verde, Vicland, and Victorgrain, a lower degree of susceptibility could be observed. Many of the uredia sporulated abundantly under humid conditions and ranked as moderately virulent. Ordinarily, however, these pustules became surrounded by chlorotic and necrotic areas and tended to desiccate soon after the infection became evident, or at least their development was markedly inhibited. The severity of infection ranged from 0 per cent on Boone, Cedar, and Texas, to 40 per cent on De Sota. The Argentinian Victoria hybrid, *Avena blanca* Klein Mar, and *Avena Amarilla* Bagé, sel. Klein \* (a selection of *Avena* Bagé 1419-36, originated in South Brazil) yielded promising results in the nurseries. Each of them scored a rust severity of 10 per cent, while the infection type belonged to the fairly mild category and only after heavy rains shifted to the moderately severe rank. The Uruguay variety exhibited intermediate reaction ranging from susceptibility to moderate resistance.

The oat varieties obtained from Finland, (Eho, Sisu, Tammi); from the Netherlands, (Adelaar, Binder, Dippés Vroege Witte, Express, Flämingsgold, Marne, warte President); from Denmark, (Picton and Prieur); the Polish introductions Antoninski, Bialy Mazur, Najwcześniejszy Niemerczanski, Proporczyk, Pulawski, niedniorychly, Rychlik Oberek, Rychlik Trybanski, Sobieszynski); and the West Australian entries (Dale, Guyra, Wongan) were all heavily damaged by *Puccinia coronata avenae*.

The results obtained in Rehovot have generally substantiated the Mikveh Israel observations, with one outstanding exception: Bond and its derivatives were free from crown rust in the Rehovot experimental trials in 1951-52.

#### CROWN RUST REACTIONS IN 1952-53

In the varietal tests conducted in 1952-53 some essential changes were introduced. A number of oat varieties, which proved to be very susceptible the previous year, were discarded and replaced by another set of varieties that had been employed in past breeding as important sources for crown rust resistance (Johnson 1953, Kehr et al. 1950, Murphy et al. 1942, Welsh et al. 1953).

The main nursery at Mikveh Israel, consisted of ninety entries. Each variety was sown in duplicates, in 18-foot rows. Notes were taken once each week.

Apart from Mikveh Israel, another seven oat nurseries were sown that season in the following places: Kefar Tabor — Lower Galilee; Kefar Vitkin — Plain of

Seed of both Argentinian varieties and information concerning their origin and parentage were kindly supplied by Dr. E. Klein.

Hefer; Masmiya Experimental Farm, located about 10 miles south of Rehovot; Mishmar Haneghev, situated a few miles north of Beersheva; Nahariya — West Galilee; Rehovot, and Sarid — Plain of Esdraelon (Figure 1). For technical reasons, our tests were confined to 23 varieties and selections, as listed in Tables and III.

#### A. Mikveh Israel trials

The results obtained in the main oat nursery, established at Mikveh Israel, are presented in Table I. They prove again that the oat varieties commonly grown in Israel, such as Fulghum, Kanota, Metulaith, and Mulga, are very susceptible to crown rust. Bond and its derivatives, (Andrew, Bonda, Camellia, Clinton, Mindo, and Shelby) rusted very heavily. The severity of infection ranged from 25 per cent on Andrew and Bond to 40 per cent on Bonda, Clinton, Mindo and Shelby, and the reaction induced by the uredia was labeled as susceptible.

Victoria derivatives yielded results similar to those obtained in 1951-52. Letoria, Neosho, Osage, and the two following varieties studied for the first time, Branch and Missouri 0-205, were susceptible and badly damaged by an attack ranging from 25 to 40 per cent severity and by uredia of the 3 and 3+ infection type. Victoria, Boone, De Sota, Fultex, Ranger, Tama, Texas, Vicland, and Victorgrain were found to be considerably more resistant and showed pustules of relatively innocuous types under dry weather conditions, whereas high humidity prompted the appearance of uredia approaching the 3+ or 3 category. The mean crown rust reactions registered on Cedar and Ventura were rated as moderately susceptible. The performance of *Avena Amarilla* Bagé, sel. Klein, and *Avena blanca* Klein Mar accorded with observations carried out in the previous growing season. Both of them ranked as moderately resistant during the major part of the season, showing type 3 pustules only when the intensity of the epiphytotic reached its climax and even then the rust severity exceeded but slightly the 10 per cent rate. Santa Fe and all the selections of Santa Fe and Clinton crosses, as listed above, proved to be very susceptible throughout the growing season. The same held true in the case of Trispermia. Ukraine was attacked by *Puccinia coronata avenae* very late, and the resulting infection was marked as 10 per cent severity and uredia type 3. The crown rust reaction recorded for Landhafer ranged from moderate resistance to moderate susceptibility, while the severity of infection amounted to 25 per cent. It was obvious that Landhafer's resistance diminished conspicuously after heading of the plants. Minnesota selections of the Landhafer  $\times$  (Mindo  $\times$  Hajira-Joanette) crosses performed in the following manner: the moderately resistant reaction prevailed in the line Minn. II-47-17; while Minn. II-47-11 and Minn. II-47-12 segregated, yielding plants affected by moderately innocuous and moderately virulent uredia. The selection Minn. II-47-8 was the least resistant, harbouring pustules of type 3 and even type 4. The Andrew  $\times$  Landhafer cross, C.I. 5685, appeared to be moderately susceptible most of the time. Thus far, of all the varieties tested only Saia was completely immune from *P. coronata avenae*.



TABLE I

Relative severity of crown rust and stem rust infection on oat varieties grown in the uniform and principal nurseries at Mikveh Israel, Israel, during the years 1951-52 and 1952-53, respectively.

Varieties concerned in the nursery trials	Rust infection and host reaction in specified oat nurseries							
	Uniform nursery 1951-1952				Principal nursery 1952-1953			
	Crown rust		Stem rust		Crown rust		Stem rust	
	Infection*	Reaction**	Infection	Reaction	Infection	Reaction	Infection	Reaction
delaar	40	S	40	S	—	—	—	—
jax	25	S	25	S	40	S	25	S
lber	40	S	40	S	25	S	25	S
lgerian	25	S	25	S	40	S	10	S
lgerian, special sel.	25	S	40	S	25	S	25	S
ndrew	40	S	25	S	25	S	40	S
ndrew × Landhafer-C.I. 5685 ***	—	—	—	—	25	MS	40	S
nthony	40	S	40	S	40	S	40	S
ntoninski	40	S	65	S	—	—	—	—
ppler	—	—	—	—	25	S	40	S
toe	40	S	40	S	—	—	—	—
vena Amarilla Bagé, sel. Klein	10	Int	25	S	10	Int	25	S
vena blanca Klein Mar	10	Int	40	S	10	Int	25	S
allidu	65	S	25	S	—	—	—	—
ankfort	25	S	25	S	—	—	—	—
earer	40	S	25	S	—	—	—	—
elar	25	S	25	S	25	S	25	S
aly Mazur	65	S	65	S	—	—	—	—
aly Orzel	65	S	65	S	—	—	—	—

Percentage of rust severity. (The degree of severity was estimated in accordance with the scale of rust severity adopted by the U. S. Department of Agriculture).

Letters indicate the following reaction classes (infection types are those of Stakman et al (Stakman et al 1944).

- I—represents immune reaction class and includes 0 and 0; infection types;  
 R—designates resistant reaction class and embraces 1 and 1+ infection types;  
 R—stands for moderate resistance and includes 3n, 3n—, 3n=, 2— to 3n, 2 to 3=, and 2+ infection types;  
 MS—denotes moderately susceptible host reactions, manifested by 3— to 3, 3= to 3, 3—, 3= infection types;  
 S—represents susceptible and very susceptible host reactions, embracing infection types: 4, 4—, 3+, and 3;  
 T—traces;  
 Int—indicates that the reaction of the variety cannot be clearly classified as resistant or susceptible.

\* C. I. refers to accession number of Cereal Crops Section, U. S. Department of Agriculture.

\*\* R.L. refers to accession number of the Rust Research Laboratory, Canada Department of Agriculture, Winnipeg, Manitoba, Canada.

TABLE I — continued (2)

Varieties concerned in the nursery trials	Rust infection and host reaction in specified oat nurseries							
	Uniform nursery 1951-1952				Principal nursery 1952-1953			
	Crown rust		Stem rust		Crown rust		Stem rust	
	Infection	Reaction	Infection	Reaction	Infection	Reaction	Infection	Reaction
Binder	40	S	25	S	—	—	—	—
Bond	40	S	40	S	25	S	25	S
Bonda	25	S	25	S	40	S	40	S
Bondvic	—	—	—	—	40	S	40	S
Boone	10	Int	40	S	25	Int	40	S
Branch	—	—	—	—	40	S	10	S
Brunker	40	S	40	S	40	S	40	S
Camellia	25	S	40	S	25	S	25	S
Canuck	25	MS-S	25	R	25	S	T	R
Carolina	40	S	40	S	40	S	40	S
Cedar	10	Int	25	S	25	Int	40	S
Clintafe	—	—	—	—	25	S	40	S
Clinton	40	S	25	S	40	S	40	S
Clinton × Marion — C.I.5647	—	—	—	—	40	S	40	S
Dale	40	S	25	S	—	—	—	—
De Sota	40	Int	25	S	25	Int	25	S
Dippés Vroege Witte	65	S	40	S	—	—	—	—
Douglas Haig	40	S	40	S	—	—	—	—
Eho	65	S	25	S	—	—	—	—
Exeter	40	S	25	S	40	S	25	S
Express	40	S	25	S	—	—	—	—
Flämingsgold	40	S	25	S	—	—	—	—
Fortune	40	S	25	S	—	—	—	—
Fulghum	65	S	40	S	65	S	40	S
Fultex	25	Int	40	S	25	Int	25	S
Glabrota	—	—	—	—	0	I	40	S
Gold Rain	65	S	40	S	—	—	—	—
Green Mountain	—	—	—	—	25	S	65	S
Green Russian	—	—	—	—	40	S	40	S
Guyra	65	S	25	S	25	S	40	S
Hawkeye	40	S	40	S	25	S	25	S
Iogold	40	S	25	S	40	S	25	S
Iowa D 67	40	S	40	S	65	S	40	S
Jinney Red	25	S	40	S	25	S	40	S
Jongensklip	40	S	25	S	25	S	40	S
Kanota	40	S	25	S	40	S	40	S
Kenya	25	S	40	S	—	—	—	—
Landhafer	—	—	—	—	25	Int	25	S
Langgewans	40	S	25	S	—	—	—	—
La Previsión 13	25	S	25	S	25	S	25	S
Larain	40	S	25	S	—	—	—	—
Legacy	65	S	25	S	—	—	—	—
Letoria	25	S	25	S	25	S	25	S
Libertas	40	S	40	S	—	—	—	—
Marion	40	S	40	S	40	S	40	S
Marne	65	S	65	S	—	—	—	—

TABLE I — continued (3)

Varieties concerned in the nursery trials	Rust infection and host reaction in specified oat nurseries							
	Uniform nursery 1951-1952				Principal nursery 1952-1953			
	Crown rust		Stem rust		Crown rust		Stem rust	
	Infection	Reaction	Infection	Reaction	Infection	Reaction	Infection	Reaction
Metulaith	40	S	25	S	25	S	25	S
Mindo	40	S	25	S	40	S	25	S
Minn. II-47-8	—	—	—	—	25	MS-S	T	R
Minn. II-47-11	—	—	—	—	25	Int	T	R
Minn. II-47-12	—	—	—	—	25	Int	T	R
Minn. II-47-17	—	—	—	—	10	MR	T	R
Minrus	40	S	25	S	40	S	25	S
Missouri 0-205	—	—	—	—	40	S	10	S
Morocco 095	25	S	25	S	—	—	—	—
Morocco 320	40	S	25	S	—	—	—	—
Mulga	25	S	25	S	25	S	25	S
Mulga 1	40	S	25	S	—	—	—	—
Mulga, sel. nigra	25	S	25	S	25	S	40	S
Najwcześniejszy Niemerczanski	65	S	40	S	—	—	—	—
Neosho	25	S	25	S	25	S	25	S
Nortex	40	S	25	S	25	S	40	S
O.A.C. — 3	40	S	25	S	—	—	—	—
O.A.C. — 720	40	S	25	S	—	—	—	—
Osage	25	S	25	S	25	S	40	S
Palestine	65	S	65	S	65	S	40	S
Picton	40	S	40	S	—	—	—	—
Prieur	40	S	40	S	—	—	—	—
Proporczyk	65	S	40	S	—	—	—	—
Pulawski-sredniorychly	65	S	65	S	—	—	—	—
Rabat	25	S	25	S	65	S	40	S
Rainbow	25	S	40	S	25	S	25	S
Ranger	10	Int	25	S	10	Int	40	S
Red Rustproof	40	S	40	S	—	—	—	—
Richland	40	S	40	S	40	S	40	S
R.L. 101 ****	40	S	25	S	40	S	40	S
R.L. 524	40	S	25	R	—	—	—	—
R.L. 2100	40	S	25	R	25	S	T	R
R.L. 2115	40	S	40	R	25	S	T	R
R.L. 2116	40	S	25	R	25	S	T	R
Rodney	25	S	25	R	25	S	T	R
Ruakura	—	—	—	—	25	S	65	S
Rusota	40	S	40	S	25	S	25	S
Rychlik Oberek	65	S	65	S	—	—	—	—
Rychlik Trybanski	65	S	65	S	—	—	—	—
Sac x Hajira — Joannette C.I. 5927	—	—	—	—	25	S	T	R
Saia	—	—	—	—	0	I	0	I
Santa Fe	—	—	—	—	40	S	65	S
Santa Fe x Clinton — C.I. 5424	—	—	—	—	25	S	40	S

TABLE I — continued (4)

Varieties concerned in the nursery trials	Rust infection and host reaction in specified oat nurseries							
	Uniform nursery 1951-1952				Principal nursery 1952-1953			
	Crown rust		Stem rust		Crown rust		Stem rust	
	Infection	Reaction	Infection	Reaction	Infection	Reaction	Infection	Reaction
Santa Fe × Clinton <sup>2</sup>	—	—	—	—	25	S	40	S
C.I. 5859	—	—	—	—	—	—	—	—
Santa Fe × Clinton <sup>3</sup>	—	—	—	—	25	S	40	S
C.I. 5951	—	—	—	—	—	—	—	—
Santa Fe × R. L. 1942 —	—	—	—	—	65	S	0	I
R.L. 144	—	—	—	—	—	—	—	—
Shelby	—	—	—	—	40	S	40	S
Sisu	65	S	65	S	—	—	—	—
Sobieszynski	65	S	65	S	—	—	—	—
South Dakota	65	S	25	S	65	S	65	S
Sterisel	—	—	—	—	65	S	65	S
Sunrise	40	S	40	S	65	S	65	S
Taho	65	S	65	S	—	—	—	—
Tama	25	Int	25	S	25	Int	40	S
Tammi	40	S	65	S	—	—	—	—
Texas	10	Int	25	S	25	Int	40	S
Trispermia	—	—	—	—	25	S	65	S
Ukraine	—	—	—	—	10	S	25	S
Uruguay	25	Int	25	S	25	MS-S	25	S
Vanguard	25	S	25	S	—	—	—	—
Ventura	25	S	25	S	40	MS	25	S
Verde	25	Int	25	S	25	Int	40	S
Vicland	25	Int	25	S	25	Int	40	S
Victorgrain	25	Int	25	S	25	Int	40	S
Victoria	—	—	—	—	10	Int	65	S
Victory	65	S	40	S	65	S	65	S
Wayne	40	S	40	S	—	—	—	—
White Tartar	—	—	—	—	45	S	25	S
Wodan	65	S	25	S	—	—	—	—
Wongan	40	S	25	S	—	—	—	—
Zwarte President	65	S	40	S	—	—	—	—

### B. Other nursery trials

Crown rust records secured from the remaining nurseries have shown that the varieties Fulghum, Metualith and Mulga were very susceptible to this disease in all trials.

Some Victoria derivatives like Branch and Missouri 0-205 were badly damaged by *P. coronata avenae*, while others, such as Boone, Ranger, Tama, Texas, Vicland and Victorgrain varied in their reaction to crown rust from moderate susceptibility at Rehovot, Masmiya and Kefar Tabor to clear resistance at Kefar Vitkin, Mishmar Hanegev, Nahariya and Sarid. *Avena blanca* Klein Mar was ordinarily resistant everywhere; only at Masmiya did 3-type infection predominate by the end of April



Bond hybrids were susceptible to crown rust at Masmiya, Rehovot and Kefar Vitkin, but at Mishmar Hanegev, Kefar Tabor, Nahariya and Sarid they harboured mainly pustules of innocuous type, whereas virulent pustules occupied an area corresponding to 10 per cent severity in the period of maximal infection. The variety Clintafe produced by crossing Santa Fe with Clinton ( $\text{Santa Fe} \times \text{Clinton}$ ) suffered severely from crown rust in all nurseries.

Selections of Landhafer  $\times$  (Mindo  $\times$  Hajira - Joannette) crosses, like Minn. I-47-12 and Minn. II-47-17 exhibited rust reactions ranging from resistance to moderate susceptibility, while the degree of severity amounted to 10 per cent. Similar results were recorded on the variety Uruguay.

The obtained data are summarized in Table II.

During the years 1953-56, inclusive oat rust uniform observation nurseries were established on average in 12 places situated in Upper Galilee, Western Galilee, Jordan Valley, Plain of Esdraelon, Plain of Hefer, Hills of Judea, Mikveh Israel Agricultural School, Rehovot, and in the southern part of the country, at the Masmiya Experimental Farm, Lakhish area and in the vicinity of Beersheba (Figure 1). Each nursery comprised 30 oat varieties and selections.

The results presenting the mean reaction types induced by crown rust on the tested varieties were fairly consistent throughout the whole period of investigation. They are assembled in Table III.

Figure 1

Distribution of oat rust observation nurseries in Israel.

Numbers indicate the regions of the country, initials stand for localities in which the nurseries were situated:

1 — Upper Galilee, 2 — Western Galilee, 3 — Lower Galilee, 4 — Valley of Esdraelon, 5 — Jordan Valley, 6 — Central Coastal Region, 7 — Hills of Judea, 8 — Negev.

K.T. — Kefar Tabor, K.V. — Kefar Vitkin (Valley of Hefer),

M. — Masmiya Experimental Farm, M.H. — Mishmar Hanegev,

M.I. — Mikveh Israel, N. — Nahariya, S. — Sarid.

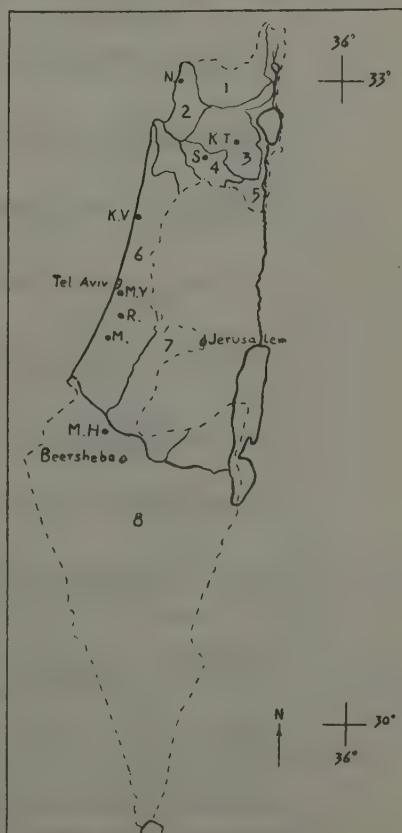


TABLE II  
*Grown first on oat varieties grown in several uniform oat nurseries in Israel in 1952-1953\**

Place Variety	Kefar Tabur Infn.	Reac.	Kefar Vikina Infn.	Reac.	Masmiya Infn.	Reac.	Mishmar Hanegiv Infn.	Reac.	Nahariya Infn.	Reac.	Rehovot Infn.	Reac.	Sarid Infn.	Reac.
Andrew	T	S	25	S	65	S	0	I	0	I	25	S	0	I
<i>Avena</i> <i>blanca</i> Klein Mar	T	R	25	R	25	Int	0	I	0	I	25	R	T	R
Bonda	T	S	25	S	40	S	0	I	T	S	25	S	T	S
Boone	10	Int	10	R	25	Int	0	R	10	R	25	Int	10	R
Branch	25	S	40	S	40	MS	10	MS	10	S	25	S	40	S
Canuck	10	MS	25	MS	25	MS	T	S	10	MS	25	MS	25	S
Clintafe	25	S	40	S	25	S	T	S	25	S	25	S	25	S
Clinton	0	I	25	S	40	S	T	S	10	S	10	S	10	S
Fulghum	40	S	40	S	40	MS	10	I	T	S	40	MS	40	S
Fultex	10	R	10	R	25	MS	0	MS	10	R	25	S	10	R
Letoria	10	S	10	S	25	S	10	MS	T	S	25	S	25	S
Metulaith	25	S	25	S	40	S	T	MS	T	S	40	S	T	S
Mindo	T	S	25	Int	40	MR	T	I	T	Int	10	MR	10	R
Minn. II-47-12	T	R	10	R	10	MR	0	I	10	Int	10	MR	0	I
Minn. II-47-17	T	MR	T	R	25	Int	T	S	Int	S	25	S	25	S
Missouri 0-205	25	S	40	S	25	S	T	I	0	I	T	R	T	R
Mulga	10	S	10	R	25	S	0	I	0	I	10	R	T	R
Ranger	10	Int	10	R	25	Int	10	I	T	S	40	Int	40	S
Rodney	40	S	40	R	40	S	10	R	T	R	25	Int	10	R
Tama	25	Int	10	R	10	Int	T	R	T	R	25	MS	10	R
Texas	10	Int	10	R	25	MS	T	R	T	MS	25	Int	10	R
Uruguay	10	MS	10	R	25	Int	10	R	10	I	25	Int	10	R
Vicland	10	Int	10	R	25	Int	10	R	0	I	25	Int	10	R
Victorgrain	10	Int	10	R	25	Int	0	I	0	I	25	Int	10	R

\* See footnotes in Table I.

TABLE III

*Reaction to crown rust and stem rust in oat rust uniform observation nurseries in Israel during the years 1953-56\**

Variety	Reaction to crown rust	Reaction to stem rust
Acre**	Seg	S
<i>Avena Amarilla</i> Bagé, sel. Klein	MR	S
<i>A. blanca</i> Klein Mar	MR	S
Bond	S	S
Burnett, C. I. 6537	S	R
Canuck	MS	R
C. I. 5685	Int	S
Clinton	S	S
Fulghum	S	S
Garry sel.— R. L. 1692-27	S	R
Landhafer	MS	S
Metualith	S	S
Minn. II-47-12	R	R
Minn. II-47-17	R	R
Mulga	S	S
Ranger	MR	S
Rehovot	R	S
Richland	S	S
R. L. 2116	S	R
Rodney	S	R
Sac × Hajira-Joanette, C.I. 1957	S	R
Saia	I	R
Santa Fe	S	S
Tama	Int → MR	S
Trispermia	S	S
T. 96***	Seg	S
Ukraine	S	S
Uruguay	Seg	S
Vicland	Int → MR	S
Victoria	Int → MR	S
White Tartar	S	S

\* See footnotes in Table I;  
Int → MR indicates that the host reaction, although mainly intermediate, was also moderately resistant for a considerable period of time;  
Seg — stands for segregation, highly resistant plants present.

\*\* This variety was erroneously labeled with the name Belar by the Acre Agric. Exp. Sta. Since it was impossible to determine the right name and origin of the variety, it is tentatively designated as Acre.

\*\*\* Received by the Acre Agric. Exp. Sta. in 1946 from the Texas Agric. Exp. Sta. The initial was given by the former, the number by the latter institution.

It became obvious that thus far the variety Saia has been completely immune from crown rust.

Both Minnesota selections : Minn.II-47-12 and Minn.II-47-17 were reselected and purified in 1951-53. Subsequently, seed secured from the most resistant plants was sown in uniform observation nurseries. The progenies have displayed extreme resistance to crown rust in all nurseries over a period of 1953-56. Similarly, both Minnesota lines appeared to be highly resistant in all greenhouse tests when artificially inoculated with about 150 isolates of *P. coronata avenae* provided from different parts of the country. Minn. II-47-17 seems to be slightly superior to Minn. II-47-12.

Victoria and its derivatives, like Cedar, Ranger, Tama and Vicland, showed intermediate reaction to crown rust ranging from moderate susceptibility to moderate resistance, the latter reaction prevailing most of the time. Bond and its hybrids were vulnerable to *P. coronata avenae* in the majority of the nurseries, while the crown rust reaction on Landhafer varied from moderate resistance in young plants to moderate susceptibility, pronounced mainly after heading.

The Argentinian varieties *Avena blanca* Klein Mar and *Avena Amarilla* Bagé, sel. Klein, retained their resistance in all plots, displaying pustules of 3-type only under very humid conditions. Santa Fe, again, appeared to be extremely susceptible, while Acre, T-96, and Uruguay comprised an appreciable number of remarkably resistant plants and hence careful selection work is very much desirable. The origin and performance of the variety Rehovot deserves a more detailed discussion. In 1951 our attention was attracted by the apparent resistance to crown rust exhibited by a number of oat plants selected in the field plot sown to the variety Mulga commonly cultivated in Israel. The seed of the most resistant plants was used in further tests in the following season and here again similar results were recorded. In the years 1953, 1954, and 1955 progenies of this new selection were included in the uniform cereal rust observation nurseries. The obtained results afforded full confirmation of the preliminary indications, as the new selection was very resistant to crown rust in all tests. It should be stressed, however, that seedlings of this selection proved to be moderately susceptible to a number of crown rust isolates under greenhouse conditions.

Since the new oat selection differs markedly in many morphologic characters from the ordinary Mulga variety and constitutes evidently a separate variety — it was tentatively named Rehovot. This variety is being tested in several experiment stations in North America, Europe and Asia. Some of the preliminary reports are encouraging, whereas in Dr. Simons' tests in Iowa it was classed intermediate in reaction under heavy epiphytotic conditions and appeared to be susceptible near the end of the season (personal communication).

Parallel to the trials conducted in the uniform observation nurseries, new oat introductions from different countries were tested in the principal nursery at Mikveh Israel.



In 1954-55 our experiments included 12 entries from Turkey: Apak — (Y-2)\*, Bozkir — (Y-1), Sari Cekoslovakya Yulaf — (Y-39), Siyah — (Y-10), Yerli selections: (Y-6), (Y-7), (Y-8), and numbered lines, Y-12, Y-30, Y-33, Y-40, Y-42. They all suffered badly from crown rust.

In 1955-56 the following 5 oat varieties obtained from the U.S.S.R. were put to test: Byzantina 11 — (*A. byzantina* C. Koch, 9992)\*\*, Byzantina 602 — (*A. byzantina* C. Koch, 9953), Byzantina 956 — (*A. byzantina* C. Koch 9954), Har'kovskiy 996 — (*A. sativa* L. var. *aurea* Körn., 8573), Sovietskii — (*A. sativa* L., var. *aristata* Kr., 8257). They proved to be extremely vulnerable to crown rust in the field plots and under greenhouse conditions. It is noteworthy that the variety Sovietskii is reported to be highly resistant to *P. coronata avenae* in the U.S.S.R. (Naumov 1955, Shevtchenko 1956, Volkov et al. 1955) with the exception of Azerbaijan and Volga regions (Naumov 1955).

#### ISOLATION OF PHYSIOLOGIC RACES OF *Puccinia coronata avenae*

Field resistance trials were accompanied in the years 1952-56 by greenhouse identification tests of crown rust specimens collected chiefly from the uniform oat nurseries. Unipustular isolates were identified with the aid of the mimeographed diagnostic keys, and differential varieties provided through the kindness of Drs. H. C. Murphy and M. D. Simons of the United States Department of Agriculture, stationed at Iowa State College, Ames, Iowa, U.S.A. The keys for identification of physiologic races of *P. coronata avenae* were later published in a series of articles (Simons 1954, 1955, Simons and Murphy 1955).

A new race of crown rust, never reported hitherto, prevailed in 1952-53 at the Mikveh Israel, Masmiya and Rehovot nurseries. The diagnostic description published elsewhere (Wahl and Schreiter 1953) shows that this race produces very virulent or moderately virulent infections on the majority of the differential varieties of the old and new sets. Only Glabrota and Saia varieties were immune from it. This new race was designated as race 264 (Simons 1954, 1955)\*\*\*. Race 264 was isolated at Mikveh Israel from Fulghum, Anthony, Bond, Boone, Landhafer, Santa Fe, Tama, Trisperina, Ukraine, Victoria, and *Avena sterilis*, at Rehovot this race attacked Fulghum, Metulaith, Bonda, Tama, *Avena sterilis*; at Masmiya race 264 was collected from Fulghum, Mulga, Tama, Vicland, *Avena sterilis*; at Mishmar Hanegev from Branch and Clinton; at Kefar Vitkin from Bonda, Clinton and *Avena sterilis*; at Sarid from Fulghum, Mulga and *Avena sterilis*; at Kefar Tabor from Fulghum and Bonda; at Nahariya from Fulghum and *Avena sterilis*.

Accession numbers furnished by the Seed Improvement Station, Eskisehir, Turkey.

\* Numbers in the brackets are those registered in the catalog of the Vsesoyusnyi Nauchno Issledavatel'skiy Institut Rasteniiovodstva, Leningrad.

\*\*\* In our earlier publications race 264 was referred to as race 276 (Wahl 1954, Wahl and Schreiter 1953). The final designation of this race was determined by Dr. Simons (1954, 1955).

Another physiologic race prevalent in some nurseries produced on the old set of differential varieties rust infections characteristic of race 56, while on the new differential varieties the following reactions were recorded:

Anthony	Very susceptible
Victoria	Very susceptible
Appler	Immune
Bond	Very susceptible
Landhafer	Very susceptible
Santa Fe	Very susceptible
Ukraine	Very susceptible
Trispermia	Very susceptible
Bondvic	Moderately susceptible
Saia	Immune

Obviously, the latter race by being virulent on Ukraine differs from race 56 isolated in Argentina to which Ukraine was resistant (Anon. 1954.) Dr. Simons is also of the opinion that the described race differs markedly from race 56, which is innocuous on Landhafer and it was designated by him as race 270 (Simons, 1954). Race 270 was isolated at Sarid from Fulghum, Branch and *Avena sterilis*; at Nahariya from Fulghum; at Haifa from *Avena sterilis*; at Mishmar-Hanegev from Branch and *Avena sterilis*. Race 270 remained very prevalent also in the following years. It was ascertained by inoculation experiments that aeciospores collected in 1955 from *Rhamnus palaestina* Boiss. in Western Galilee and from *Rhamnus alaternus* L. in Jerusalem, produce on oats crown rust uredia identified as race 270. At least 2 uredial isolates of this race derived from the aecia of *Rhamnus alaternus* yielded readily and consistently telia on Fulghum seedlings, about 5 days after the appearance of uredia.

In 1953 and 1954 crown rust race 276, first discovered in Argentina (Simons 1955) ranked in Israel as one of the most predominant. Race 276 is virulent on all differential varieties except Victoria and Saia and can be distinguished from race 264 by its lack of aggressiveness on Victoria, whereas the latter host is moderately vulnerable to race 264. This distinction between races 264 and 276 is not always clear cut. We have learned that the susceptible reaction of Victoria seedlings induced by race 264, perceptible at the early stage of disease development, about 11-13 days after inoculation, may be altered to an intermediate or even resistant one when pustules of mildly virulent type become surrounded by sandy-pinkish necrotic areas and desiccate eventually. This frequently recorded phenomenon can be considered as manifestation of delayed resistance. The fact that the difference between races 264 and 276 is not always well-defined brought Simons to the conclusion that the separation of those races in 2 distinct biological entities is not yet sufficiently justified (Simons 1955). Our experience with race 264 accords with Simons' observations and conclusions.

Race 277 determined originally in Argentina (Simons 1955) was isolated here

5 times in 1956. This race is virulent on all differential hosts but Victoria, Bond, Ukraine and Saia (Simons 1955).

The affinity between some of the prominent crown rust races of Israel and Argentina is of theoretical and practical significance and merits further elucidation.

#### STEM RUST REACTIONS

Preliminary oat stem rust observations were initiated at Mikveh Israel in 1950-51, repeated at the same place and at Rehovot in 1951-52, and continued in uniform observation nurseries in 1952-53. The data recorded during the last two years are set out in Tables I and IV. It is obvious, that in all our trials stem rust epiphytotics started by mid-April and reached their peak in May. Our common varieties, Fulghum, Kanota, Metulaith, and Mulga were vulnerable to *P. graminis avenae* and yet the early maturing oats were not severely damaged, since they seemingly escaped the devastating effects of stem rust attack. The same varieties, when sown late, suffered very badly. The preponderant majority of oats tested was susceptible to stem rust, judging by the 100 per cent prevalence, high severity, and infection type classified as virulent. A notable exception were Saia and varieties containing the so-called Canadian factors for oat stem rust resistance, such as the numbered lines R.L. 144, R.L. 524, R.L. 2100, R.L. 2115, R.L. 2116, Canuck, Rodney, the selection of Sac  $\times$  Hajira-Joanette (C.I. 5927), and the Minneota selections of Landhafer  $\times$  (Mindo  $\times$  Hajira-Joanette), like Minn. II-47-8, Minn. II-47-11, Minn. II-47-12, Minn. II-47-17. All the above listed varieties were tested in the principal nursery at Mikveh Israel during the years 1953-56 inclusive, and some of them, such as Saia, Canuck, Rodney, Minn. II-47-12, Minn. II-47-17, Sac  $\times$  Hajira-Joanette, became permanent components of the uniform nurseries throughout the entire period of investigations. They proved to be so far extremely resistant to stem rust. At the end of the growing season moderate infection of small uredial pustules could be observed, but this late appearance of the pathogen does not seem to reduce yields.

From 1953 onward the uniform nurseries comprised also the varieties Burnett — C.I. 6537 (known also as Clinton  $\times$  Ukraine\*), and Garry sel. — R.L. 1692-27. Both varieties have displayed highly resistant reactions to stem rust.

White Tartar and varieties possessing White Russian type of stem rust resistance, such as Anthony, Bonda, Clinton, Mindo and Minrus rusted severely in the field plots.

Oat varieties involving the Richland-Rainbow-Iogold type of resistance factors, like Ajax, Andrew, Branch, Exeter, Fortune, Hawkeye, Iogold, Missouri 0-205, Rainbow, Richland and Vanguard harbored stem rust pustules of the 3+ and 4 type, while the severity of the infection varied from 10 per cent to 65 per cent.

Ukraine oats, tested for 5 years in the principal nursery and for 3 years in the uniform nurseries, remained in the fields free from stem rust until mid-May, while

\* The designation Clinton  $\times$  Ukraine is not correct since the parentage of Burnett is (Victoria  $\times$  Hajira-Banner)  $\times$  Cole. (Dr. H. A. Rodenhiser, personal communication).

TABLE IV  
*Stem rust on oat varieties in several uniform nurseries in Israel, in 1952-1953\**

Place	Kefar Tabor	Kefar Vitkin	Masmiya	Mishmar Hanegev	Nahariya	Rehovot	Sarid
Variety	Inf.	Reac.	Inf.	Reac.	Inf.	Reac.	Inf.
Andrew	25	S	25	S	65	S	10
Avena blanca Klein Mar	40	S	40	S	65	S	40
Bonda	25	S	25	S	65	S	10
Boone	25	S	40	S	65	S	25
Branch	25	S	25	S	25	S	25
Canuck	T	R	0	I	0	I	T
Clintafe	25	S	25	S	40	S	40
Clinton	40	S	40	S	25	S	25
Fulghum	25	S	25	S	25	S	40
Fulrex	25	S	25	S	65	S	25
Ietoria	25	S	25	S	40	S	25
Metulath	40	S	40	S	65	S	40
Mindo	40	S	25	S	65	S	10
Minn. II-47-12	T	R	T	R	T	R	T
Minn. II-47-17	T	R	T	R	T	R	T
Missouri 0-205	25	S	25	S	25	S	25
Mulga	25	S	25	S	25	S	40
Ranger	25	S	25	S	40	S	40
Rodney	T	R	T	R	T	R	T
Tama	25	S	40	S	40	S	25
Texas	25	S	40	S	40	S	25
Uruguay	40	S	40	S	65	S	25
Vicland	25	S	25	S	25	S	25
Victorgrain	25	S	25	S	25	S	25

\* See footnotes in Table I.



later in May the susceptibility of Ukraine increased conspicuously, the severity of infection exceeding 25 per cent, and pustules belonging to 3 and 4 type.

All the remaining oat varieties listed in Tables I, III, IV were rendered extremely susceptible to stem rust. The variety Sovietskyi, resistant to stem rust in the U.S.S.R. (Naumov 1955) was severely affected by *P. graminis avenae* in greenhouse tests and in field trials. The same was true of other oat varieties introduced from the U.S.S.R. and Turkey, as listed above.

#### ISOLATION OF PHYSIOLOGIC RACES OF *Puccinia graminis avenae*

The initial identifications of the physiologic races of oat stem rust occurring in Israel were carried out by Drs. E. C. Stakman and M. N. Levine at the Federal Cereal Research Laboratory in Minnesota.

The uredial material from which the isolates was provided by Dr. I. Reichert and Eng. G. Minz during the years 1926-1938, inclusive. The rust specimens were collected in widely separated parts of the country. Levine and Smith (1937) referred to the presence of races 2, 6, and 7 in Israel. According to a recent communication from Dr. Levine, the following 5 physiologic races of *Puccinia graminis avenae* were isolated from the early Israeli collections, namely 1, 2, 6, 7, and 8. Of these, race 6 constituted 30.4%; race 2 was second in order of frequency of occurrence with 23.1%; while each of the remaining three races accounted for about 15.4% of the total number of isolates identified.

In our identification work, unipustular isolates of rusted oat specimens, collected chiefly at the observation nurseries, were studied. The identification of the stem rust races isolated was determined with the aid of the diagnostic keys published by Stakman, Levine, Christensen and Isenbeck (1935) and by Newton and Johnson (1944), on the basis of reactions produced on the standard differential hosts.

Thirty stem rust collections were furnished in 1951-52 by the Mikveh Israel nursery, comprising infected specimens of varieties possessing White Russian type of resistance, such as Bonda, Clinton, Mindo and Minrus, and of oat plants endowed with the Richland-Rainbow-Iogold resistance factors. The identification tests revealed that race 6 of *P. graminis avenae* predominated, being three times as frequent as race 8. Twenty collections secured from the Rehovoth experimental plots consisted of races 6 and 8 in the approximate proportions of three to one. In 1952-53 the stem rust identification studies were further continued and collections obtained from most nurseries examined. The results of these trials are assembled in Table V.

Likewise, stem rust samples of affected wild oat species, *Avena sterilis*, collected from various regions of the country in 1951-52 and 1952-53 consisted of races 6 and 8, race 6 being in the forefront. Our identification studies of the physiologic specialization of *P. graminis avenae* were carried on during the years 1953-56. Over 150 isolates collected from all parts of the country were identified.

TABLE V

*Geographic distribution and frequency occurrence of two prevailing physiologic races of oat stem rust (*Puccinia graminis avenae*) isolated from specimens collected in uniform observation nurseries grown in various parts of Israel during the growing season of 1953*

Geographic distribution	Frequency occurrence of specified races			
	Race 6	Race 8	Number of isolates in given places	Per cent of total number of isolates
Kefar Tabor	—	2	2	7.4
Kefar-Vitkin	2	1	3	11.1
Masmiya	3	2	5	18.5
Mikveh Israel	5	—	5	18.5
Mishmar-Hanegev	3	—	3	11.1
Nahariya	3	—	3	11.1
Rehovot	4	—	4	14.9
Sarid	2	—	2	7.9
Total number of isolates identified	22	5	27	—
Relative percentage of occurrence	81.5	18.5	—	100.0

Race 6 comprised approximately 97 per cent of the total number of isolates, and race 8 was second in prevalence, while race 3 occurred only once over the entire period of investigation.

In our identification tests in addition to the 4 standard differential varieties: Bond, Richland, Sevnothree and White Tartar, seedlings of Burnett—(C.I. 6537), Canuck, Garry sel. (R.L. 1692-27), Rodney, Saia, Minn. II-47-12, and Minn. II-47-17 were employed. All accessory varieties proved to be extremely resistant. Their resistance broke down when the tests were performed at temperatures above 28°C approximately. Only Saia constituted a notable exception, since it exhibited resistance at lower as well as at higher temperatures, exceeding 28°C.

The general preponderance of the most destructive race 6 is very significant. A somewhat similar situation was reported from Germany (Johnson and Newton 1946) and recently from Peru (Postigo et al. 1958).

#### DISCUSSION AND CONCLUSIONS

Studies on crown rust and stem rust of oats reported herein have been conducted over a period of 1951-56, inclusive. Severe damage caused to oats by rust epiphytotics made it imperative to explore means and measures for saving this crop from rust hazards. The results obtained seem to be of theoretical and practical importance, since they prove the validity and soundness of certain principles and procedures generally employed in phytopathological research, and on the other hand gained for us a number of very promising oat varieties.

The universally adopted method for combating cereal rusts is based on the introduction or production of resistant varieties. This part of research is usually integrated with pathological studies involving the physiologic specialization of the parasitic organisms. Both methods were applied in our endeavours to control oat rust diseases.

Over 150 oat varieties and selections were tested in the principal nursery at Mikveh Israel; some of them were also investigated in the uniform cereal rusts observation nurseries distributed throughout the country. It was ascertained that the local oat selection Rehovot is extremely resistant in the fields to crown rust. Some of the foreign introductions, such as the Brazilian variety Saia and the Minnesota selections of Landhafer×Mindo×Hajira-Joanette)—Minn. II-47-12, Minn. II-47-17 proved to be highly resistant to crown rust and stem rust in greenhouse tests and field trials. Both Minnesota lines underwent reselection and purification during 4 growing seasons. Saia is thus far immune from crown rust, highly resistant to stem rust, and very suitable for fodder and hay production (Wahl and Menkes 1957). The so-called Canadian factors for oat stem rust resistance have afforded effective protection against *P. graminis avenae*.

The progress achieved in these studies attests to the importance of international cooperation in fighting plant diseases. Such a collaboration is generally recognized as useful and beneficial to all participants (Stakman 1954).

The conspicuous affinity of crown rust races in Israel and Argentina presents an interesting problem and calls for a closer collaboration in cereal rusts research between both countries. The recently reported appearance of oat stem rust race 4 in Argentina (Vallega 1954), which is closely related to our omniprevalent race 6, emphasizes the need for this kind of cooperation.

The fact has been established that a number of the crown and stem rust races prevailing in Israel are highly virulent; this explains too the aggressiveness of our oat rusts epiphytotic. Some of the crown rust races, e. g. race 264 and 270 were first identified in this country.

The predominance of extremely destructive physiologic races of oat rusts is of paramount interest. Obviously, coincidence did not create this situation; it is rather an outcome of a process of evolution of organisms closely associated for a very long time. The elucidation of the factors and principles underlying this phenomenon pose a challenge to plant pathology, and may shed light on the problem of evolution of parasitic organisms.

Any attempt to solve this query is bound to bring into account the generally accepted hypothesis that certain varieties of cultivated oats are derived from the wild species *Avena sterilis*, indigenous to the Mediterranean region (Findley 1956, Stanton 1936, Vavilov 1949-50). *Avena sterilis* thrives abundantly in Israel, its Hebrew name "common oats" is indicative of the wide distribution of this plant. *Avena sterilis* rusts heavily and is affected by crown and stem rust races identi-

cal to those secured from cultivated oat varieties. Despite severe rust infection the wild oats do not seem to suffer from the disease, they show excellent tolerance to both rusts.

*Rhamnus alaternus* and *R. palaestina* are important constituents of the Mediterranean vegetation in Israel. This is of great significance in view of the findings described herein and elsewhere (Rayss and Habelska 1942), that aecia produced on those plants belong to the life-cycle of *P. coronata avenae*. They gave rise to at least one extremely virulent race, number 270, never identified in other countries hitherto.

Rusts as obligate parasites, show a pronounced specialization in their ability to adapt themselves to a particular suspect, and the presence of a congenial host is indispensable for their existence. Hence it is conceivable that oats and oat rusts originated in the same geographic area, and that the evolutionary development of the host influenced profoundly the evolutionary course of the crown rust and stem rust fungi.

According to a common assumption, cereal rusts were very destructive to crops in the Land of Israel already in the early Biblical era. It is only natural to expect that the long-lasting host-parasite struggle for survival resulted in the persistence of the "fittest" host characterized by a high degree of tolerance to its enemies, and in the development of some of the very specialized parasite rust races endowed with unusual virulence.

Our findings concerning physiologic specialization of *P. coronata avenae* and *P. graminis avenae* support this hypothesis. It is noteworthy that the most virulent oat stem rust race 6 comprised about 97 per cent of the total number of isolates identified by us, and was also collected so far from 14 additional genera of wild grasses (K. Z. Gerechter, unpublished data).

A similar concept of evolution of plant parasites was tested and verified by investigators of potato late blight in Mexico (Mills and Niederhauser 1953; Niederhauser, Cervantes and Servin 1954). The far-reaching accord in conclusions inferred from studies on *Phytophthora infestans* and both oat rusts carried out in the centers of origin of the respective suspects implies a confirmation of a general principle.

Most likely, the spectrum of physiologic races of oat rusts in this area, outstanding for their virulence, constitutes an advanced stage of an evolutionary process, that presumably can be attained also in other oat growing regions in the more or less distant future.

For this reasons, testing of agricultural crops in the centers of their origin, where the presence of extremely aggressive and virulent parasitic races of their pathogens is very probable, may provide the plant breeder with important information for assessing the potentialities and the protective value of the genetic factors for disease resistance incorporated in the breeding material.



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A REVISION OF STERNBERGIA (AMARYLLIDACEAE)  
IN PALESTINE

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ABSTRACT

The species of *Sternbergia* growing in Palestine are: *S. clusiana* (Ker-Gawl.) Ker-Gawl. ex Sprengel, syn. *S. spaffordiana* Dinsmore; *S. colchiciflora* Waldst. et Kit., which is very rare; and *S. lutea* (L.) Ker-Gawl. ex Sprengel, syn. *S. auran-tiaca* Dinsmore, which is doubtfully indigenous. Their synonymy and distribution are discussed and a key comprising all species of the genus provided.

*Sternbergia* is a small genus of bulbous plants belonging to the family Amaryllidaceae and possessing yellow flowers which in general appearance resemble those of *Crocus* but have six stamens as well as other less obvious distinguishing features. Waldstein and Kitaibel (1803-04) founded the genus on a new species collected by them in Hungary, naming this *Sternbergia colchiciflora* in honour of the Bohemian botanist, Count Caspar von Sternberg (1741-1837). This species had, however, been first described and illustrated two centuries earlier by the Flemish botanist Charles de l'Écluse (Carolus Clusius) in his *Rariorum Plantarum Historia* 164 (1601) under the name *Narcissus autumnalis minor* together with two other species named by him *Narcissus persicus* (which is now *Sternbergia clusiana*) and *Narcissus autumnalis major* (which is now *Sternbergia lutea*). Clusius's work is, of course, pre-Linnaean but it has an important bearing on subsequent nomenclature. Thus Linnaeus in 1753 cited Clusius's *Narcissus autumnalis major* under *Amaryllis lutea* L. which is the basionym of *Sternbergia lutea* and Ker-Gawler also cited Clusius's work when in 1808 he published the name *Amaryllis clusiana*.

There has been much difference of opinion about the species of *Sternbergia* occurring in Palestine. Boissier in 1882 recorded only one, *S. clusiana*, represented by Roth's specimens from Jaffa and Jerusalem. Post in 1896 cited this as being found (in 1891) by Hart on Mount Hor (Edom). Eig in 1927 recorded *S. colchiciflora* var. *aetnensis* (Guss.) from Upper Galilee and later (1933) listed three species for Palestine as a whole: *S. clusiana*, *S. spaffordiana* Dinsm. and *S. colchiciflora* var. *aetnensis*. Dinsmore had described *S. spaffordiana* in 1928 as

a new Palestinian species. In his 1933 revision of Post's Flora he recorded four species for Palestine: 1. *S. macrantha* J. Gay; 2. *S. spaffordiana* Dinsm.; 3. another new species, *S. aurantiaca* Dinsm., very close to *S. lutea*; 4. *S. colchiciflora*.

For some years one of us (N. Feinbrun) has studied the genus in Palestine with both living and herbarium material and was able during 1953 to study in addition the herbarium material at the Herbarium of the Royal Botanic Gardens, Kew; the British Museum (Natural History) had no Palestinian material of *Sternbergia*. The other (W.T. Stearn) has supplemented this taxonomic work by a study of the relevant older literature. The results are given below. The following key covers all the species of the genus *Sternbergia*, but only the Palestinian species are discussed.

### Key for the identification of *Sternbergia* species

1. Tube of perigonium as long as or only slightly shorter than its segments. Peduncle not longer than bulb-neck. Seeds strophiolate 2
  - Tube of perigonium much shorter than its segments. Peduncle produced from the bulb-neck. Seeds not strophiolate 4
2. Plant small. Leaves 3-5 mm broad. Perigonium segments linear, 1-3½ cm long, 3-5 mm broad 3
  - Plant large. Leaves about 1 cm broad. Perigonium segments oblong-ovate, 3½-7 cm long, 1-3½ cm broad.
3. Leaves appearing after the flowers. S. clusiana (Ker-Gawl.) Ker-Gawl. ex Sprengel
  - Leaves appearing together with the the flowers. S. colchiciflora W. et K.
- 4 (1). Flowers appearing in autumn (September-October) together with the leaves or a short time before the leaves; ovary sessile. Central and S. Europe, Eastern Mediterranean. S. pulchella Boiss. et Bl.
  - Flowers appearing in spring (March) together with the leaves; ovary and capsule stipitate. E. Transcaucasia and Iran. S. lutea (L.) Ker-Gawl.
- S. fischeriana (Herb.) Rupr.

**1. *Sternbergia clusiana* (Ker-Gawl.) Ker-Gawl. ex Sprengel, Syst. Veg. 2 : 57 (1825); Schultes et Schultes fil. in Roemer et Schultes, Syst. Veg. 7 (2) : 794 (1830); Boiss., Fl. Orient. 5:148 (1882).**

*Narcissus persicus* Clusius, Rar. Pl. Hist. 163 (1601).

*Amaryllis clusiana* Ker-Gawl. in Curtis's Bot. Mag. 27 : sub t. 1089 (1808) amend. in J. Sci. Arts 2:345 (1817).

*Oporanthus clusianus* Herbert, Appendix 38 (1821).

*S. stipitata* Boiss. et Hausskn. in Boiss., Fl. Orient. 5:148 (1882).

*S. macrantha* Gay ex Baker, Handb. Amaryll. 28 (1888); Baker in Curtis's Bot. Mag. 122 : t. 7459 (1896).

*S. spaffordiana* Dinsmore in Fedde, Repert. Sp. Nov. 24:302 (1928); Post, Fl. ed. 2, 2:607 (1933); Feinbrun, Zohary and Koppel, Fl. Land Israel 2 (1952).

*Illustrations*: Clusius, *Rar. Pl. Hist.* 163 (1601); Curtis's *Bot. Mag.*: t. 7459 (1896); Feinbrun, Zohary and Koppel, *Fl. Land Israel* 2 (1952).

*Specimens examined*: PALESTINE: Jerusalem, IX-X. 1860 Hooker and Hanbury (Kew); Jaffa, Roth (Kew); Edom, Mt. Hor and Petra, XI. 1883 Hart (Kew); Zizeh (Moab) 720 m. XI. 1911 Meyers and Dinsmore m 834 (leaves in I. 1912 grown in Jerusalem; Kew); Upper Galilee, Jebel Jermak ca 1000 m, 1950 Feinbrun (HJ). LEBANON: Cedars, 7.XI.1935 and 13.XI.1935 R. Aaronsohn (Herb. Aaronsohn). SYRIA: in agro p. Aleppo, II. 1867 Haussknecht (sub. *S. latifolia* Boiss. et Hausskn., Kew). ASIA MINOR: Defilé des Portes Ciliciennes 11.X.1885 Balansa 827 (Kew; holotype of *S. macrantha* Gay); Cilician Taurus, Bulgar Dag, Gülek 3800'—4800', frequens, X.1853 Kotschy 344 (Kew); Kurn Dag, Zeitun, Cataonia 5000', steep limestone scree, 10.V.1934 Balls and Gourlay (Kew); Whittall, 391 V.1875 (specimen figured in *Bot.Mag.* under *S. macrantha*; Kew). PERSIA: Kurdistan sept., inter Sungur et Dinawer, 1867 Haussknecht (Kew; isotype of *S. stipitata* Boiss. et Hausskn.).

Boissier in 1882 recorded *S. clusiana* from several East Mediterranean countries (Palestine, Syria, Lebanon and Asia Minor) and cited *S. macrantha* Gay as a synonym. Baker, however, in 1888 raised doubt as to the identity of Ker-Gawler's *S. clusiana* with Boissier's. He accordingly adopted Gay's manuscript name *S. macrantha* and gave "*S. clusiana* Boiss. non Ker", as a synonym. Dinsmore in his revision of Post's *Flora* (1933) accepted Baker's opinion.

What then is the true *S. clusiana*?

The basis of this name is a plant described and figured by Clusius in 1601 from living specimens that had come originally from Constantinople, the accompanying label "*Zarem cada persiano*" indicating that they had reached Constantinople from Persia. Certainly no plant similar to Clusius's *Narcissus persicus* grows wild near Constantinople. A woodcut showing two bulbs, one leafless but in flower, the other with four erect twisted leaves, accompanied his account. In 1808 Ker-Gawler listed Clusius's *Narcissus persicus* as a synonym of *Amaryllis colchiciflora*, this being a new combination based on *Sternbergia colchiciflora* for he never accepted *Sternbergia* as a genus distinct from *Amaryllis*. At the same time he published the name *Amaryllis clusiana*, citing as a synonym *Narcissus autumnalis minor* of Clusius, which is, however, the same as Waldstein and Kitaibel's *Sternbergia colchiciflora*. It is clear the synonyms were inadvertently transposed. Ker-Gawler may have muddled his notes or the printer may have misunderstood the manuscript; certainly the printed record makes no sense and is contrary to his intention. In 1817 he published in the Royal Institution's *Journal of Science and the Arts* 2: 342-371 a "review of the genus *Amaryllis*". Here he corrected his earlier *Bot.Mag.* citations; here *Narcissus autumnalis minor* is placed under *Amaryllis colchiciflora* and *Narcissus persicus* under *Amaryllis clusiana*.

It can be argued that the name *Amaryllis clusiana* of 1808 was based on *Narcissus autumnalis minor* and hence is a synonym of *Sternbergia colchiciflora* and that the name *Amaryllis clusiana* of 1817 is based on a different type (*Narcissus persicus* Clus.) and is thus a later homonym to be rejected as illegitimate. Ker-



Gawler's *Amaryllis clusiana* of 1817 was not, however, published as a new name; he simply corrected a printing error of his earlier work. Later authors have consistently taken this view and it would indeed be contrary to commonsense and the intent of the International Code of Botanical Nomenclature to reject the epithet *clusiana* on this account.

In 1825 Sprengel published a brief summary of the genus *Sternbergia* in which he included six species, cited as *colchiciflora* Kit., *clusiana* Ker, *exigua* Ker, *citrina* Ker, *lutea* Ker, *americana* Hofmannsegg. Thus *clusiana* was here transferred to *Sternbergia* as a species distinct from *colchiciflora*. Why Sprengel cited Ker-Gawler as the authority for the epithets *exigua* (based on *Amaryllis exigua* Schouesboe), *citrina* (based on *Amaryllis citrina* Sm.) and *lutea* (based on *Amaryllis lutea* L.) is not clear.

It is also hard to understand what caused Baker in 1888 to identify Clusius's drawing of *Narcissus persicus* with *Sternbergia colchiciflora*. Although he states under *S. colchiciflora* that "*Narcissus persicus* Clus. Hist. II. 163 (*S. clusiana* Ker) is evidently this species", the woodcut clearly portrays the species which Baker called *S. macrantha*, agreeing with both in the proportions of the leaves and the shape of the perigon-segments. The specimens cited by Boissier agree with Clusius's drawings of *Narcissus persicus* and Baker's coloured plate of *Sternbergia macrantha* in Curtis's Bot. Mag., t. 7459. They also correspond with the Palestinian plants known to one of us (N. Feinbrun) in a living state. Thus there is every reason to conclude that these Palestinian plants belong to *S. clusiana*.

Further it is also clear that *S. spaffordiana* Dinsm. is synonymous with *S. clusiana*. The late J. E. Dinsmore not only gave N. Feinbrun a few bulbs of his *S. spaffordiana* but kindly accompanied her to the very place on the outskirts of Jerusalem where he had collected his *S. spaffordiana*.

*Sternbergia stipitata* Boiss. et Hausskn. is also synonymous with *S. clusiana*. Iso-type material at Kew differs from typical *S. clusiana* only in having somewhat smaller flowers; specimens with flowers smaller than the average were found by N. Feinbrun on Jebel Jermak (Upper Galilee). Stipitate perigon divisions, mentioned by Boissier as characteristic of *S. stipitata*, are shown in Dinsmore's figure of his *S. spaffordiana* in Post's Flora.

The above list of specimens examined can be supplemented by the following records in the literature. PALESTINE : N. of Madaba (Moab), Nablus (fide Post-Dinsmore 1933). LEBANON and SYRIA : Zahleh, Ehden, Damascus (fide Post-Dinsmore 1933). S. TURKEY : Marash, Amanus (fide Bornmüller 1917), Killis in Turkey and Aleppo in N. Syria (Nabelek 1923). PERSIA : Choremadabad (fide Bornmüller 1908, under *S. stipitata*).

The geographical area of *S. clusiana* thus comprises Palestine (Cis- and Transjordan), Syria, Lebanon, Asia Minor and N. Persia. In Palestine *S. clusiana* was found in Upper Galilee, Samaria, Judean Mountains, Moab and Edom. Baker also

mentioned the Sinai Peninsula, but apparently had in mind Hart's plant from Mt. Hor (Edom). It is doubtful whether Dr. Roth actually collected *S. clusiana* near Jaffa, where edaphic conditions are quite different from those characteristic of the habitat of *S. clusiana* (limestone rocks and terra rossa). Moreover, as is evident from other specimens collected by Roth, his labels were not always accurate.

Clusius's 1601 account provides the first record of the cultivation of *Sternbergia clusiana* in European gardens. It seems not to have been re-introduced until E.J. Whittall of Smyrna sent bulbs to Kew in 1894, from one of which the coloured plate in Curtis's Botanical Magazine, t. 7459, was made.

**2. *Sternbergia colchiciflora*** Waldst. et Kit., Descr. Icones Pl. Rar. Hung. 2 : 172, t. 159 (1803-04).

*Narcissus autumnalis minor* Clusius, Rar. Pl. Hist. 164 (1601).

*Amaryllis colchiciflora* (Waldst. et Kit.) Ker-Gawl. in Curtis's Bot. Mag. 27 : sub t. 1089 (1808).

*A. etnensis* Raf., Carat. 84, t. 18 f. 3 (1810), Chloris 12 (1815) as *A. aetnensis*.

*Oporanthus colchiciflorus* (Waldst. et Kit.) Herbert, Appendix 38 (1827).

*Sternbergia aetnensis* (Raf.) Gussone, Fl. Sic. Prodr. 1:395 (1827).

*S. colchiciflora* var. *aetnensis* (Raf.) Rouy in Bull. Soc. Bot. France 31:182 (1884).

*Illustrations* : Clusius, Rar. Pl. Hist. 164 (1601); Waldstein and Kitaibel, Descr. Icones Pl. Rar. Hung. 2: t. 159 (1803-04); Bot. Reg. 23: t. 2008 (1837); Reichenbach, Icones Fl. Germ. 9 : t. 372 f. 823-24 (1847); Fiori, Iconogr. Fl. Ital. 93 (1921); Bull. Herb. Boiss. 5 t. 13 (1898); Javorka & Csapody, Iconogr. Fl. Hung. t. 7 (1929).

*Specimen examined* : PALESTINE: Lower Galilee, Beit Keshet, north of Mt. Tabor, 195 m., XI.1956 J. Katznelson.

Until now Eig's 1927 record of *S. colchiciflora* from Kfar Gileadi in Upper Galilee has been the only one for the region covered by Post's Flora. Our new record is from a locality further south, actually the southernmost point for the range of the species, which comprises Hungary, southern Italy, Dalmatia, Macedonia, Greece, Crimea, the Caucasus, Anatolia and northern Palestine. No records for Lebanon or Syria have yet been published. Mr. J. Katznelson states that near Beit Keshet the plant grows both on Pliocene rock, in soil pockets, and on Eocene, among *Poterium spinosum*. Specimens kindly provided by Mr. J. Katznelson and grown in Jerusalem developed leaves and fruits.

The flowers of *S. colchiciflora*, as a rule, rise only slightly above the ground. Gorshkova in the Flora USSR 4:489 (1935) quotes a 1925 report by Troitski that the flowers of this species sometimes develop to maturity within the bulb, the young fruits rising later above the ground, where they ripen.

In Palestine the plant is rare. It seems that either it does not flower every year or it remains invisible during flowering owing to its cleistogamous habit. At any

rate N. Feinbrun searched for *S. colchiciflora* in vain for several years and, although told that it grew near Mt. Tabor, failed to get it until last autumn (1956).

Eig (1927) identified his specimen with var. *aetnensis* (Guss.), using the characters given by Fiori (1923). It seems that in *Sternbergia* this variation in the shape and width of the perigonium divisions does not justify the recognition of a separate taxon and we follow Boissier who placed *S. aetnensis* (Raf.) Gussone as a synonym of *S. colchiciflora*.

**3. *Sternbergia lutea* (L.) Ker-Gawl. ex Sprengel, Syst. Veg. 2: 57 (1825); Schultes et Schultes fil. in Roemer et Schultes, Syst. Veg. 7 (2):795 (1830).**

*Narcissus autumnalis major* Clusius, Rar. Pl. Hist. 164 (1601).

*Amaryllis lutea* L., Sp. Pl. 1:292 (1753).

*Oporanthus luteus* (L.) Herbert, Appendix 38 (1821).

*Sternbergia aurantiaca* Dinsmore, Pl. Dinsm. 2 (1933); Post, Fl., 2nd. ed., 2:607 (1933).

*Illustrations*: Clusius, Rar. Pl. Hist. 164 (1601); Curtis's Bot. Mag. 9: t. 290 (1795); Redouté, Liliac. 3: t. 148 (1807); Sibthorp et Smith, Fl. Graeca 4: t. 310 (1823); Reichenbach, Icones Fl. Germ. 9: t. 373 (1847); H.S. Thompson, Fl. Pl. Riviera t. 28 (1914).

*Sternbergia lutea* is probably not indigenous in Palestine. N. Feinbrun has never found it in a natural habitat. Some of her specimens were given her by Dinsmore and some she found in an abandoned Arab garden in Jerusalem.

It is recorded from most Mediterranean countries, e.g. Algeria, Spain, southern France, Italy and Dalmatia; it also grows in eastern Transcaucasia, northern Persia and mountainous Central Asia. In the Kew Herbarium there is a specimen from Central Asia which seems somewhat different from typical *S. lutea*. Hayek (1933) mentions that *S. lutea* is also grown for ornament ("etiam ornamentia culta") and Battandier and Trabut (1895) record it as being found "ca et là, près des jardins et des cemetières arabes; spont.?" Thus it is not impossible that Arabs from other Mediterranean countries introduced *S. lutea* into Jerusalem. Dinsmore also cites a plant recorded by Decaisne from between Damascus and Ba'albek.

In Jerusalem *S. lutea* usually flowers in October, sometimes before the leaves appear. *S. lutea* is, however, usually described as synanthous. In this connection the paper by Amico (1947) is important.

Amico experimented with bulbs of *S. lutea* collected from natural habitats in Italy. He was able to show that the vegetative and reproductive phases of the plant are independent. By taking the bulbs out of the soil in May and keeping them at 30° C in vapour-saturated air he provoked the appearance of the leaves as early as June instead of September. Under these conditions their flowering was completely suppressed. By changing the treatment, i. e. by keeping the bulbs in an aerated atmosphere and at natural temperature during one month and successively

treating them in vapour-saturated thermostat, Amico succeeded in provoking the appearance of leaves without suppressing the flowering.

Amico concludes that a resting period in a dry atmosphere is necessary to realize the full cycle of growth, vegetative and reproductive, in *Sternbergia*.

It is evident that while in Italy natural humidity during September is sufficient to cause leaf growth in *S. lutea*, the necessary conditions for the appearance of leaves are realized as late as November in Palestine, whereas the flowers appear here independently in October, in much drier conditions. *S. lutea* produces leaves and flowers together in Jerusalem when kept well-watered.

Dinsmore in Post's Flora 1933 remarks that his *S. aurantiaca* strongly resembles *S. lutea* Ker-Gawl. "but the leaves come after the flowers. Apparently wild". As shown above, this character changes with changing humidity and *S. aurantiaca* cannot be separated taxonomically from *S. lutea*.

The experimental results of Amico throw some doubts as to the distinctness of *S. pulchella* and *S. fischerina*, the former being related to *S. colchiciflora*, the latter to *S. lutea*.

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## ISOLATION OF *LABYRINTHULA MACROCYSTIS* FROM SOIL\*

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### ABSTRACT

A species of *Labyrinthula* has been isolated from roots of a diseased plant (*Carica papaya*) in the Jordan Valley. It has been shown that this *Labyrinthula* is able to survive in ordinary garden soil for at least a month and to infect the roots of mustard and wheat plants growing in this soil by penetrating the root-hairs. In the one experiment carried out, the development of infected plants was not inferior to that of uninfected plants growing under the same conditions. A simple method for the continuous cultivation of this organism on agar medium has been described and the use of certain bacteria or yeasts as food organisms evaluated.

The organism has been identified with *Labyrinthula macrocystis* Cienkowski.

### INTRODUCTION

Members of the genus *Labyrinthula* have been reported from the European and American coasts of the Atlantic Ocean, from the Pacific Ocean, from the Mediterranean Sea and from fresh water (Cienkowski 1867, Zopf 1892, Dangeard 1910 and 1932, Valkanov 1929, Young 1943, Watson and Raper 1957). In most cases the organisms were found in these water-habitats on living plant material. No *Labyrinthula* has been recorded so far from soil. Renn (1936) held a *Labyrinthula* responsible for the so-called wasting disease of eelgrass (*Zostera marina*) which devastated at that time large stretches of this useful and ecologically important plant in the Atlantic Ocean. This claim was supported by Young (1943) who confirmed the preliminary results of Renn and identified the etiologic agent of the wasting disease as *Labyrinthula macrocystis* Cienkowski. *Labyrinthulae* are potential plant-parasites and as the example of the wasting disease indicates they may occasionally be responsible for considerable material damage. Relatively little is known about their life history in nature, and also the question of their systematic position is far from settled: Parker and Haswell (1947) express the opinion that *Labyrinthulae* might be related to the Foraminifera, Smith (1955) finds similarities with certain Chrysophyceae, while Zopf (1892) and Dangeard (1932) think of them as a kind of primitive Myxomycetes and place them together with the Acrasiales in the class of Protomyxidae.

The present report describes the occurrence of a *Labyrinthula* in soil and deals with the ecological and taxonomic aspects of this finding.

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\* Dedicated to Professor Dr. Paul Buchner, Porto d'Ischia (Napoli).

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## EXPERIMENTAL

1. *Technique of isolation of the Labyrinthulae from soil*

The sample of soil which contained our organism was taken from the roots of a diseased *Carica papaya* plant in Kinnereth, in the Jordan Valley.

Pieces of the roots together with adhering soil were placed on water agar consisting of agar-agar (strips) 2% in tap water. After an incubation period of 3 days at room temperature, a few strands of spindle-shaped cells moving along a network of fine filaments were noted among the various moulds, bacteria and protozoa which developed in the same plate. A piece of such a strand which had migrated to a part of the plate free from contaminating organisms was cut out aseptically, together with the adhering agar, and transferred to a new water agar plate. In the vicinity of this piece were streaked several loopfuls of *Escherichia coli* from an agar culture to serve as food material. It was assumed that migrating cells from the explanted piece would reach the streaks of *E. coli* and that this bacterium would be a suitable food for them. This assumption was correct. The spindle cells multiplied rapidly in the bacterial mass and, after exhaustion of this food-source, formed a large number of cyst-like cell aggregations, so called sori (Figure 3). The morphology of the cells and especially their ability to form a net plasmodium characterize our organism as a *Labyrinthula* species (Figures 1 and 2).

From the invaded streaks of *E. coli* or other food organism, as will be described later, the *Labyrinthula* could be transferred to other agar plates and kept so continuously in the laboratory. Transfers were made at intervals of 2 to 3 weeks.

2. *Nutritional requirements of the isolated Labyrinthula*

Besides *Escherichia coli* other bacteria and various yeast cultures were tried as food organisms. *Labyrinthula* grew well also with *Aerobacter aerogenes*, *Bacillus subtilis*, *Micrococcus albus*, *Sarcina flava* and *Serratia marcescens*, that means with Gram-positive as well as Gram-negative types. There was, however, one noteworthy exception: *Pseudomonas aeruginosa* was left untouched, the *Labyrinthula* cells being obviously inhibited by some substance diffusing out of the growth streaks of this bacterium. Other species of *Pseudomonas* whose pigment formation was less developed were attacked by *Labyrinthula*, but they too seemed to be less suitable as food than other Gram-negative bacteria.

The feeding experiments reported here were carried out on plates of tap water agar.

Different results were obtained when the food organisms were placed on agar media made with nutrient solutions instead of tap water.

On a medium containing glucose 1%,  $(\text{NH}_4)_2\text{SO}_4$  0.2%,  $\text{K}_2\text{HPO}_4$  0.1% and  $\text{Mg SO}_4$  0.05%, that means a carbon and nitrogen source but no vitamins, the *Labyrinthula* grew with *Rhodotorula pallida* as food organism but not with *Rhodotorula mucilaginosa*, although both these species supported growth equally well on the

water agar plate. Most other organisms when tested on the glucose mineral salt medium proved like *Rh. mucilaginoso* to be unsuitable as food organisms for our *Labyrinthula*.

If the medium contained, besides glucose and the ammonium salt, also yeast extract, all the bacteria and yeast cultures tested, including *Rh. pallida*, were unsuitable. *Labyrinthula* failed to multiply in their presence and died in a rather short time. Without other micro-organisms on these plates there was some multiplication, although a limited one which after some time ceased altogether.

To integrate these observations into one single explanation we venture the following theory: *Labyrinthula* is able to attack other micro-organisms if they are in an inactive state, that means if they are not metabolising. This condition is fulfilled on the tap water agar which lacks food material for an active metabolism of bacteria or yeasts. The different behaviour of *Rh. pallida* and *Rh. mucilaginoso* on the medium containing glucose and ammoniumsulphate is perhaps due to differences in the vitamin requirements of the two yeasts. Our strain of *Rh. pallida* is unable to grow without pyridoxin and thiamine. It is therefore attacked on the glucose mineral medium like on the tap water agar. *Rh. mucilaginoso* needs thiamine but is able to a limited degree to grow also without this growth factor. This may be sufficient to protect the yeast on this medium against the attack of the *Labyrinthula*. On the yeast extract medium both species are actively metabolising and are therefore equally unavailable for the *Labyrinthula* cell. Yeast extract agar is obviously not sufficient as a culture medium for continuous growth.

### 3. Salt tolerance and temperature range of our cultures

As most of the *Labyrinthulae* described were found in sea water, we examined the tolerance of our organism towards different salt concentrations. A series of agar media were prepared in which instead of tap water various mixtures of tap and sea water were used. *Rhodotorula pallida* served as food organism.

The *Labyrinthula* grew in this experiment on all the mixtures which contained 80% sea water or less, but not on higher concentrations. When, however, the *Labyrinthula* from the agar plate with 80% sea water was transferred to a new set of plates, it grew readily also on the plate made with 100% sea water. The sea water used had a salinity of 40 S‰. Higher concentrations were not tested. Subcultures from plates with 100% sea water did not grow at first on plates with tap water, but again one single transfer to a medium with an intermediate salt concentration was sufficient to adapt the organism for growth on tap water agar.

The range of temperatures tolerated by our organism is similar to that described for *L. macrocystis* (Young 1943, Vishniac 1955). The optimum range of growth was 20-25°C, but cultures remained alive for some time also at 35°C. However, 12 hours at 38°C were sufficient to kill all the cells.

#### 4. Morphology and taxonomic position of our organism

There is complete agreement in all morphological aspects of our organism and the *L. macrocystis* as described by Young. It is therefore not necessary to give here a detailed description. We shall, however, mention one point which is relevant for a discussion of taxonomic questions in this genus:

In preparations stained with Giemsa stain there were striking differences in the appearance of various cells from the same culture. The cytoplasm of some cells was stained lightly and more or less homogeneously, while in others it contained numerous dark-stained inclusions. Cells with such inclusions looked definitely like organisms which ingested a large number of bacteria. As long as our *Labyrinthula* was fed on cells of *E. coli*, it was indeed rather difficult to decide whether the bacteria were digested intra- or extra-cellularly. Ingestion of particulate matter has been reported for a *Labyrinthula* by Dangeard (1910) and a new species *L. Zopfii* was created on this account. When yeast cells served as food, similar inclusions were found. But the yeast cells could easily be differentiated from these inclusions by their larger size and they were never found inside the *Labyrinthula* cells. The inclusions therefore are not ingested food particles.

#### 5. *Labyrinthula* as soil inhabitant

As has been explained already, the sample of soil which contained our strain of *Labyrinthula* had been taken from the roots of a diseased plant (*Carica papaya*). It was, therefore, of interest to ascertain as far as possible whether *Labyrinthula* was the cause of disease in this plant, and whether in general *Labyrinthula* is able to attack land plants in the same way as has been reported for water plants.

The disease in the papaya plant unfortunately could not be followed up, as the plant had been uprooted at the time our sample was taken, but we were able to make some observations concerning the behaviour of *Labyrinthula* towards other land plants.

Seeds of *Sinapis alba* were placed without sterile precautions on a tap water agar plate. After the seedlings had germinated and grown a root of several centimeters length, the plate was inoculated with cells from a net plasmodium.

The spreading *Labyrinthula* cells attacked the various micro-organisms which developed around the roots of the seedling, but penetrated also into the rootlets and from there into cells of the cortex (Figures 4 and 5). The invasion remained rather restricted in its extent and there was no sweeping spread as has been described for the leaves of *Zostera marina*. The cells of *Labyrinthula* inside the plant tissue formed cysts which fitted neatly into the cells of the cortex or sometimes also those of the root-hair and remained in this stage without change during the whole time of observation, i.e. about 2 weeks (Figures 6 and 7). The infection experiment was then repeated with plants growing in soil. In each of two flower pots with ordinary garden soil a few seeds of *Sinapis alba* and grains of wheat were planted. The pots

were kept near a well-lighted window in the laboratory, and the seedlings developed without any sign of etiolation. When the mustard seedlings had developed their first leaves, cysts of *Labyrinthula* were added superficially to the soil in one of the pots, while the second remained untreated and served as control. After 3 weeks two mustard plants, together with their roots, were carefully removed from the pot to which *Labyrinthula* had been added. The roots were washed in running water in order to remove the adhering soil as far as possible, and roots as well as stems were then cut into pieces of about  $\frac{1}{2}$  cm each and placed separately on tap water agar plates.

From most of the root pieces there was after 2 days an outgrowth of *Labyrinthula* cells, while the stems remained sterile or gave rise only to bacterial or fungal growth.

Thirty days after the addition of *Labyrinthula* cysts to the soil, a wheat plant was removed in the same way and part of its root-system cultivated. The culture was positive for *Labyrinthula*, but the infection was obviously less widespread than in the case of the mustard plants. Only two root pieces from the ten which we examined were infected.

The remaining plants were observed for another month in order to see whether the infected plants showed any symptoms of disease or were in any way inferior to the control plants in soil without *Labyrinthula*. No such symptoms were discovered and the plants continued to develop normally. We should like to add here that the detection of *Labyrinthula* in cultures from plant tissues is sometimes difficult owing to heavy development of bacteria around the explanted pieces of root on the agar plate. If, however, after 24 or 48 hours incubation on the agar plate the pieces were transferred to a second agar plate, the growth of *Labyrinthula*, if present, became very conspicuous. It seems that the easily diffusible food material in these pieces which gives rise to the heavy development of bacteria is exhausted after this time and the inactive bacteria which still remain on the root surface do not impede the excystment and development of the *Labyrinthula*.

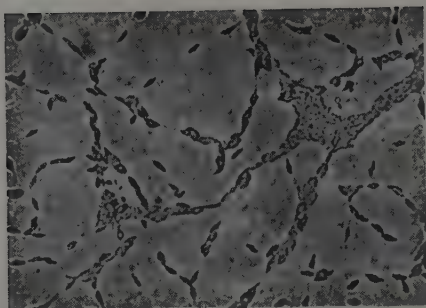
#### DISCUSSION OF RESULTS

The infection experiments proved that our *Labyrinthula* is able to penetrate the roots of cultivated plants like white mustard or wheat and to form cysts in the root tissue. The plants which harboured the *Labyrinthula* cells in their root system did not show any external sign of damage and their development did not appear to be inferior to the non-infected plants. However, the number of plant species tested as well as the number of plants in each experiment was rather small, so that it can not be decided whether *Labyrinthula* is harmless to land plants under all circumstances. As the methods and media necessary for detection and isolation of *Labyrinthula* are different from those commonly used in phytopathology, it is possible that *Labyrinthulae* are more frequently inhabitants of plant roots than has been found up to now.

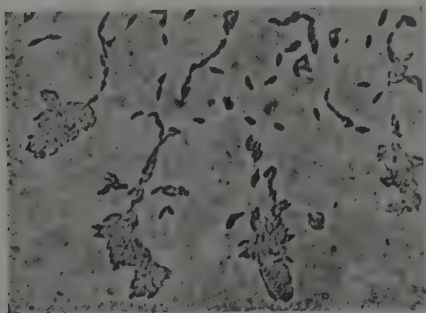




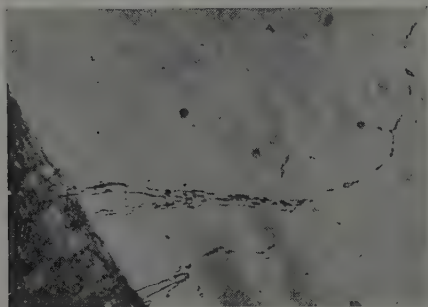
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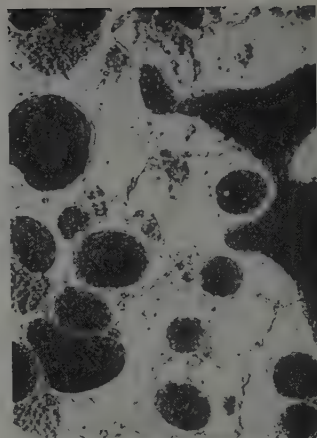
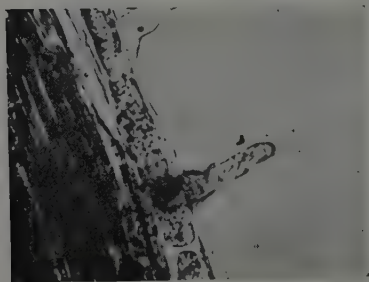
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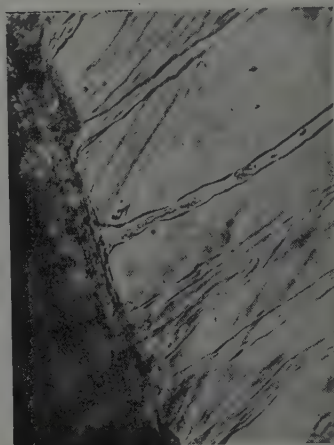
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Although our *Labyrinthula* has been found in a new habitat, it is obviously not necessary to ascribe it to a new species. The growth experiments have shown that this organism is able after very short adaptation to live in the same salinity as most of the other species do. The soil from which it was isolated had been irrigated with water from the Jordan River, and it is possible that this river or Lake Kinnereth constitute the original habitat for this organism. As in all other respects it conforms to the description of *Labyrinthula macrocystis*, we believe it to belong to this species.

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## EXPLANATION OF FIGURES

The life-history of a *Labyrinthula* from soil.

## Figure 1

Part of the pseudoplasmodium of *Labyrinthula macrocystis* on tap water agar. ( $\times 200$ ).

## Figure 2

Accumulation of cells at the periphery of the pseudoplasmodium. ( $\times 200$ ).

## Figure 3

Formation of cysts (sori) on tap water agar. ( $\times 100$ ).

## Figure 4

Strands of *Labyrinthula* cells entering the root-hairs of a young mustard plant (*Sinapis alba*) on tap water agar. ( $\times 100$ ).

## Figure 5

The same as Figure 4. ( $\times 200$ ).

## Figure 6

A root of *Sinapis alba* containing cysts of *Labyrinthula* in the cells of the cortex. ( $\times 350$ ).

## Figure 7

Cysts of *Labyrinthula* in the root of *Sinapis alba*. One cyst extending into the root-hair. ( $\times 350$ ).

# DEW ABSORPTION BY PLANTS OF ARID ZONES

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## ABSTRACT

1. A series of plants was examined for dew absorption, for which purpose the V-method was adapted. By this method dew absorption can be calculated from differences in water content or water saturation deficit of dew-exposed as against dew-protected arms of a V-shaped branch not detached from the plant.
2. On the basis of their capacity to absorb dew, the plants were divided into two groups, pronounced absorbers and non-absorbers.
3. So far no difference was found in the intensity of dew absorption between Mediterranean and desert plants.
4. Soil humidity affects dew absorption; the latter is considerably higher under dry soil conditions than under irrigation.
5. The recorded amounts of dew absorbed by the plants seem to be of little value in balancing their daily water output.

## INTRODUCTION

The problem of dew absorption by aerial plant organs has been studied recently by Krause (1935), Brierley (1936), Stone, Went and Young (1950), Arvidsson (1951), Meidner (1954), Steubing (1955), Stone (1957) and others. So far, no general conclusions can be drawn from the inadequate and often controversial data available (Stone 1957). Only a few of the studies deal with plants that are regularly subjected to extreme summer drought and at times show sublethal saturation deficits for prolonged periods. And it is under those very conditions that one may expect dew to be of vital importance to plants in improving their water balance. The experiments reported below were made in an attempt to test this assumption.

## MATERIAL AND METHODS

A number of Mediterranean evergreen trees and shrubs, as well as some desert plant species native to Israel, were examined for absorption of dew by their aerial organs. The experiments were carried out during the dry summer months under both natural and artificial conditions, in localities where large amounts of dew are deposited on plants, and where the number of dew nights per annum exceeds one hundred (Ashbel 1951, Duvdevani 1953).

For dew absorption measurements a method, which we called the V-method, was adapted. By this method the water content and the water saturation deficit were determined on a V-shaped branch which had a more or less equal number of leaves on its two arms (Figure 1). Shortly after sunset a sample of leaves was taken from each arm of the V-branch, and water content and/or water saturation deficit were

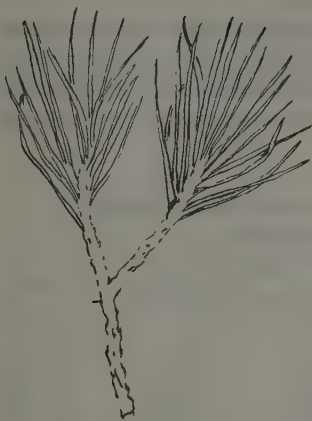


Figure 1

A V-branch of *Pinus halepensis*

determined. Then one arm of each V-branch, chosen at random, was covered with a plastic bag to prevent dew deposition, while the other was left uncovered, exposed to dew\*. At sunrise, leaf samples were again taken from both arms of the V-branch, and after being wiped were examined for water content and/or saturation deficit. This method takes into consideration two sources of moisture increment in leaves during dew nights: soil water absorbed through the roots, and dew absorbed by the aerial organs. Our assumption is that any excess of water in the exposed arm of a V-branch, as against the covered one, must be ascribed to dew absorption only, though no conclusions as to the exact quantities involved can be drawn.

Each sample in our experiments included three leaves in *Ceratonia*, *Olea*, *Polygonum*, *Lycium* and *Zygophyllum*; three groups of five brachyblasts in *Pinus*; or three twigs in *Retama*, *Thymelaea*, *Kochia*, *Haloxylon*, *Salsola*, *Artemisia* and *Anabasis*. The water content was determined by drying the samples in an oven at 80°C for 24 hours. The water saturation deficit was measured by the modified method of Stocker (1929), i.e. petioles of the leaves were first immersed in water for 24 hours, and then dried as above. Three to five specimens of each species were examined and on each plant three to five V-branches were treated.

The amounts of dew deposited on an iron cube and on the upper surface of a living, horizontally situated, leaf of *Ficus elastica* were parallelly measured during some of the experiments and the results are given in Table I.

TABLE I  
Dew condensation during nights of experiments

Date	Dew condensation on upper surface of an iron cube 10×10×10 cm (mg/cm <sup>2</sup> )	Dew condensation on upper surface of a <i>Ficus elastica</i> leaf (mg/cm <sup>2</sup> )
26.VIII.1954	5.1	2.8
7. IX. 1954	9.8	5.8
8. IX. 1954	9.6	6.4
16. IX. 1954	11.4	6.7

\* In our later experiments (1955), this arm, instead of being left exposed to dew, was sprayed and afterwards also covered with a plastic bag in order to equal the conditions and prevent evaporation on dry nights.

## EXPERIMENTS AND RESULTS

*Experiment 1.* In this experiment (Beersheva, Northern Negev, 1955) fourteen species were examined for dew absorption by the V-method. The results are presented in Table II. As seen from this Table, the plant species examined can be divided into two groups, according to their dew absorption capacity. The species in

TABLE II  
Means of morning water content of V-branches, expressed in percentages  
of the previous evening water content

Plant examined	Morning		Difference	P *
	Exposed arm	Covered arm		
Pronounced absorbers				
<i>Lycium arabicum</i>	116.7	106.6	10.1	P < 1%
<i>Salsola inermis</i>	129.4	104.8	24.6	P < 5%
<i>Salsola vermiculata</i>	116.9	106.0	10.9	P < 1%
<i>Zygophyllum dumosum</i>	119.0	109.4	9.6	P < 1%
Non-absorbers				
<i>Anabasis articulata</i>	101.3	100.1	1.2	not significant
<i>Artemisia monosperma</i>	98.6	98.9	—0.3	"
<i>Haloxylon articulatum</i>	103.2	98.8	4.4	"
<i>Noëa mucronata</i>	106.3	92.7	13.6	"
<i>Peganum harmala</i>	106.0	103.7	2.3	"
<i>Polygonum equisetiforme</i>	103.8	102.1	1.7	"
<i>Retama raetam</i>	100.0	100.1	—0.1	"
<i>Salsola austrani</i>	105.8	97.4	8.4	"
<i>Thymelaea hirsuta</i>	106.5	98.1	8.4	"

\* P is the corresponding probability obtained from Student's t-table.

which the water increment ascribed to dew was significant, were defined as pronounced dew absorbers. The second group, of non-absorbers, comprises all the species in which no significant differences between, or even lower values in, the exposed as against the protected arm were recorded. The negative results were due to the excess of night transpiration, as measured in a previous experiment, over dew absorption. This division corresponds to the findings of Krause (1935), though his definition is slightly different.

The moisture taken in by leaves as dew may pass from saturated branches to non-saturated ones (Brierley 1936). Thus the question arises, whether the figures obtained in the above experiment indicate the actual dew absorption of the plant. In the case of the supposed non-absorbers, it may be objected that the more or less equal amount of water recorded in both the exposed and covered arms is not to be ascribed to an absence of absorption, but to the transfer of water from the exposed arms to the covered ones. To test this objection *Kochia indica*, a supposed non-absorber, was reexamined in two ways: (a) by testing the water saturation de-



ficit in ten entire plants, five of which — chosen at random — were left exposed to dew, while the other five were covered, and (b) by the V-method (Table III). As shown in this Table, no differences in water saturation deficit were recorded in covered as against exposed specimens nor in covered as against exposed branches. From this it may be concluded that *Kochia indica*, at least, is a true non-absorber.

TABLE III  
*Evening and morning water saturation deficit percentages in Kochia indica*  
(a) Entirely exposed and covered plants

	Evening		Morning	
	Exposed	Covered	Exposed	Covered
	49.9	50.3	49.8	49.0
	46.5	45.7	46.2	56.3
	49.5	49.7	53.8	49.0
	45.6	44.9	55.5	51.0
	51.5	50.6	52.1	56.0
Mean	48.6	48.2	51.4	52.2

(b) Exposed and covered arms of V-branches

	Evening		Morning	
	Exposed arm	Covered arm	Exposed arm	Covered arm
	48.4	48.3	51.8	52.4
	45.0	49.9	48.2	45.7
	46.0	45.3	49.5	54.3
	50.1	45.9	55.3	55.5
	51.0	45.9	55.8	48.5
Mean	48.1	46.9	52.1	51.2

There remains the objection regarding the dew absorbers that the amount of dew absorbed, as expressed by the differences in water content between the two arms of a V-branch, is smaller than the actual amount of dew absorbed, due to the transfer of moisture from the exposed to the covered arm. However, this seems unlikely, in view of the fact that the comparatively small water deficiency in three covered branches of the examined plants is not outbalanced by the passage of water from the numerous other exposed branches of the same plant. Thus, water transfer from one brach to another in the plants examined, if it occurs at all, must be very slow.

*Experiment 2.* In this experiment (Jerusalem, 1954) the decrease in water saturation deficit during a dew-night was determined by the V-method on adult trees of two Mediterranean species, *Olea europaea* and *Pinus halepensis* (Table IV). This Table shows a considerable decrease in saturation deficit in the branches exposed to dew, as compared to the covered ones. The decrease must be ascribed mainly to dew absorption, as the experiment was performed under dry summer

TABLE IV  
*Evening and morning water saturation deficit percentages in  
 V-branches of two Mediterranean tree species*  
 (Figures given are mean values of three plants each)

Plant examined	Date	Evening	Morning		Difference*
			Exposed arm	Covered arm	
<i>Pinus halepensis</i>	8.IX.54	22.8	12.5	18.9	6.4
" "	"	23.3	9.9	21.9	12.0
" "	16.IX.54	22.6	17.4	21.8	4.4
<i>Olea europaea</i>	7.IX.54	8.4	4.0	7.5	3.5
" "	"	12.9	7.6	11.4	3.8
" "	"	23.3	9.3	21.6	12.3

\* Analysis of variance has shown a significant difference at 5% level between the means of the plants treated.

conditions. It was found, however, that within the range of saturation deficits recorded in this experiment, the overnight absorption of moisture by leaves did not exceed an average of 100 mg per 1gm fresh weight. Such an amount is hardly sufficient to cover the loss of water caused by twenty to thirty minutes of transpiration (Poljakoff 1945, Lifschitz 1953). In none of our experiments did dew absorption lead to a full recovery from the saturation deficit. Thus, as regards the water balance of these plants, the recorded amount of water absorbed as dew is not likely to be of value. Whether or not it plays any role in the life of these plants remains an open question.

*Experiment 3.* In this experiment (Jerusalem, 1954) two- to four-year old saplings of *Ceratonia siliqua*, *Pinus halepensis*, *Atriplex halimus*, *Zygophyllum dumosum*, *Pistacia lentiscus* and *Olea europaea*, all grown in watered tin containers, were examined for the water content of their leaves. The soil water content at the time of the experiment was approximately at field capacity. The results are given in Table V. This Table shows the higher moisture content of the exposed leaves as against the covered ones, and demonstrates the fact that the plants absorbed dew, although they were profusely irrigated. Moreover, as the soil moisture conditions were equal for all the species investigated, the results point to the different ability of these species to absorb dew. This confirms the opinion of Marloth (1926), Krause (1935), Stalfelt (1944) and others that the amount of dew absorbed varies largely with the species. No differences could be seen in dew absorption capacity of Mediterranean as against desert species.

On comparing dew absorption by irrigated *Pinus* saplings (Experiment 3) with dew absorption by adult non-irrigated *Pinus* trees (Experiment 2), lower absorption values were arrived at for the former than for the latter. In a following experiment, therefore, we compared dew absorption under soil dry conditions to that under irrigation.

TABLE V

*Means of morning water content of V-branches, expressed in percentages of the previous evening water content*

Plant examined	Morning		Difference*
	Exposed arm	Covered arm	
<i>Atriplex halimus</i>	117.0	109.3	7.7
<i>Ceratonia siliqua</i>	121.2	114.1	7.1
<i>Olea europaea</i>	117.9	104.7	13.2
<i>Pinus halepensis</i>	133.8	120.5	13.3
<i>Pistacia lentiscus</i>	118.6	106.3	12.3
<i>Zygophyllum dumosum</i>	130.8	118.9	12.0

\* Analysis of variance has shown a significant difference at 5% level between the means of the plants treated.

*Experiment 4.* In this experiment (Jerusalem, 1954) the V-method was used to reveal the effect of soil moisture in the root region on the ability of leaves to absorb dew. For this purpose six two-year old *Ceratonia siliqua* saplings, of more or less equal size, were grown in tin containers. Three of them were heavily irrigated, the remainder were left exposed to drought until their leaves began to shrivel and the soil moisture content dropped below the wilting point. The results are given in Table VI.

TABLE VI

*Means of morning water content of V-branches in not irrigated and irrigated Ceratonia siliqua saplings, expressed in percentages of the previous evening water content*

Plant treatment	Morning		Difference*
	Exposed arm	Covered arm	
No irrigation	112.2	103.9	8.3
"	117.3	106.1	11.2
"	115.8	105.9	9.9
Irrigation	121.2	114.1	7.1
"	120.8	114.3	6.5
"	118.9	110.6	8.3

\* Analysis of variance has shown a significant difference at 1% level between the means of plants and treatments.

A glance at the results recorded in the above Table shows that, at least under the conditions of our experiment, dew absorption by the plants exposed to drought was higher than that by the plants grown under irrigation. This goes to emphasize that the overnight water supply through the roots counts in dew absorption considerations. This is where the V-method has its advantage over methods which use detached organs and yield data not necessarily representing the actual dew absorption by intact plants.

We may conclude from our experiments that dew absorption varies with the plant species, and is dependent on intensity and duration of dewfall as well as on soil moisture conditions.

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## LETTER TO THE EDITOR

### Germination behaviour of some halophytes

Differences in salt tolerance between germinating seeds and adult plants are well known (Hayward and Wadleigh 1949). Inhibition of germination by concentrated salt solutions may thus exclude plants from portions of their potential distribution area and constitute a major factor of plant zonation in saline habitats.

In order to prove whether or not a correlation exists between salt tolerance of plants in germination and salinity of their natural habitat, the following investigation, on sixteen of the most common halophytes, was undertaken.

The seeds were germinated in a series of M NaCl solutions with a gradual increase of concentration from distilled water to 1M. Two of the species were additionally germinated in M  $\text{CaCl}_2$  solutions. The germination experiments were carried out at 20°C in the dark and in continuous light; three species were also germinated at 30°C.

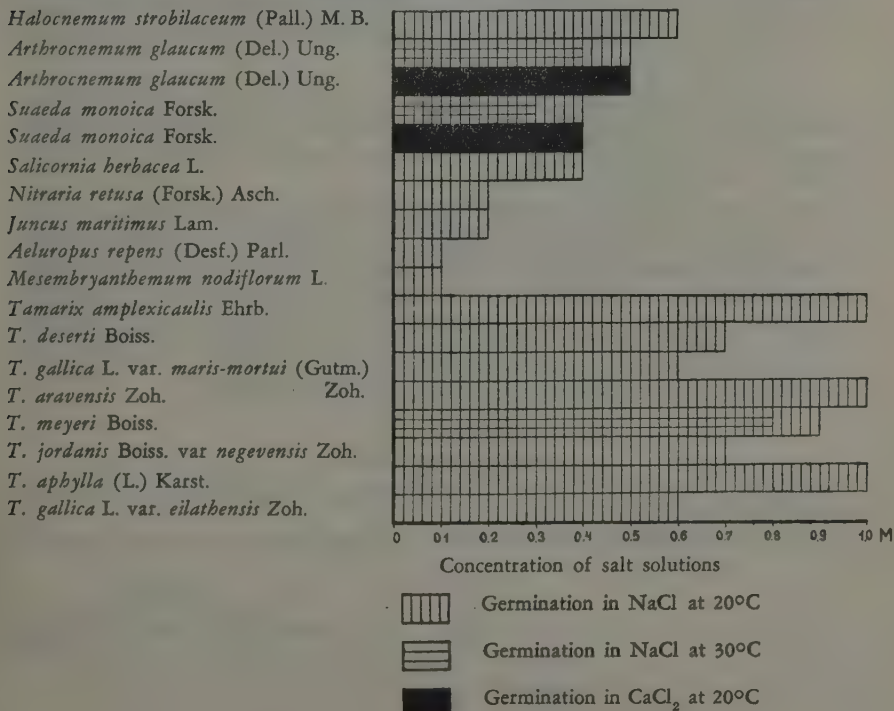


Figure 1

Salt tolerance in germination of halophytes.



Petri-dishes could not be used for the germination experiments, as the rapid drying out of the solutions caused a steep rise in their concentrations within a few hours. The following method was, therefore, adopted: A glass jar (5cm diameter), containing 50 cc of the desired solution, was used. A metal-celluloid net, supported by a cork-ring, was floated on the solution. The seeds were placed on the net and thus came in contact with the solution by their lower surface only. The increase in concentration of the salt solutions during the experiment did not exceed 2% of the initial concentration. The results are given in Figure 1.

It is evident from the above figure that the *Tamarix* species dealt with form a separate group exhibiting a very high salt tolerance in germination (cf. Litwak 1955). The lowest tolerance shown by any of the *Tamarix* species is equal to the highest tolerance of the other species investigated. A direct correlation between the salt tolerance in germination of the *Tamarix* species and the salinity of their respective habitats cannot be demonstrated. For instance, *Tamarix aphylla*, a non-saline dune and wadi plant, has a similar salt tolerance in germination as *Tamarix amplexicaulis* growing in the most saline places on the shores of the Dead Sea. The *Tamarix* species are, therefore, not limited to their respective habitats by their salt tolerance in germination.

All the other species investigated show a correlation between their salt tolerance in germination and the salinity of the habitat, i.e., plants from saline zones have a higher salt tolerance in germination than plants from less saline zones.

No differences were found in the two species investigated as to their ability to germinate in NaCl and CaCl<sub>2</sub> solutions of equal molar concentrations. This agrees well with Schratz (1934) and Ayers (1952).

Seed germination in each treatment was independent of light or darkness. Similar results were obtained by Beadle (1952) for five species of *Atriplex* in Australia. Of the sixteen species investigated, only *Juncus maritimus* revealed a sensitivity to light, i.e., much higher germination percentages were obtained in the dark than in continuous light (cf. Koller 1956) within the same range of salt tolerance.

Germination at 30° C was not inhibited in the three species investigated — *Arthrocnemum glaucum*, *Suaeda monoica* and *Tamarix meyeri* — although the range of salt tolerance became narrower. This conforms with the findings of Ahi and Powers (1938). Thus, at least in these species, summer germination could be possible, as far as temperature is concerned. However, during the summer months the salt concentration in the soil is too high. For this reason germination only takes place in winter, when the salt concentration in the soil is lowered by increased moisture, which is in accordance with the opinion of Chapman (1942).

As to the salinity of the respective habitats the reader is referred to M. Zohary and Orshansky (1949), Orshan and D. Zohary (1955) and M. Zohary (1956).

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